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Dr. J.S. Scott (at right) greeting the Right Honourable Edward Schreyer during the Governor General's 1983 visit to the St. Andrews Biological Station. Mr. P.A. Koeller appears in the background.

James Stuart (Hamish) Scott (1924–2010)

A prolific and well-known fisheries scientist in Atlantic Canada, Hamish Scott died on 12 March 2010 while visiting his hometown of St. Andrews, Scotland.

After service with Royal Navy during the Second World War, Hamish completed his undergraduate studies at St. Andrews University, where he majored in geology. His early academic studies and prowess resulted in his recruitment to an important survey of the Nepalese Himalayas, bringing him into contact with two of the most recognized climbers in history: H.W. (Bill) Tilman (the expedition leader and author) and the Sherpa Tenzing Norgay, one of the first two individuals to reach the summit of Mount Everest. The survey was a 4-month exploratory and scientific expedition to the Langtang, Ganesh, and Jugal regions in Nepal, in the early stages of that country's re-opening to outsiders.

Hamish's interests then moved towards fish population ecology. During a 10-year period in Malaya, he worked with the British Colonial Government and published a monograph on the sea fishes of Malaya (Scott 1959). He earned a Doctorate in parasitology at St. Andrews University in 1963 (his thesis described the postembryonic development of a cestode larvae, *Paricterotaenia paradoxa*) and worked with the British Government doing fishery development work in Nigeria for 3 years. Hamish then settled with his family in St. Andrews, New Brunswick, Canada, in late 1967, where he began his career at the St. Andrews Biological Station.

Hamish's work in the 1960s focussed on classic fish population ecology, including studies of the meristics and morphometrics, feeding, and population structure of silver hake (*Merlucius bilinearis*) and northern sand lance (*Ammodytes dubius*; Scott 1968). Hamish also contributed to our understanding of Atlantic argentine (*Argentina silus*), describing aspects of their early life history. In this period and during the subsequent decade, much of Hamish's work focussed on what was considered at the time to be commercially under-utilized species. In that manner, his work helped address what was a substantial gap in our knowledge of the Canadian Northwest fish fauna.

During the late 1960s and the early part of the 1970s, Hamish and fellow scientists within the Groundfish Section of the Department of Fisheries and Oceans (DFO) invested considerable effort in the establishment of depth-stratified random

surveys of groundfish populations on the Scotian Shelf and Bay of Fundy, with the first conducted in 1971. These annual surveys, intended to provide insight into the distribution and abundance of a broad range of marine fish species, continue to be a critically important source of information on the status of Canadian Atlantic fish fauna and their associated environment. Hamish extended the surveys to the relatively shallow waters around Sable Island during 1980–1985, addressing a limitation of the surveys (Scott 1982*b*).

During the 1980s, Hamish demonstrated the value of the survey series by publishing findings on the depth, temperature, and salinity preferences of common fish of the Scotian Shelf (Scott 1982*a*), the selection of bottom type by groundfish (Scott 1982*c*), and using matrix analyses to document the seasonal co-occurrence of groundfish species on the Scotian Shelf (Scott 1989). Hamish also co-authored an extensive and authoritative technical report describing the seasonal spatial distributions of groundfishes of the Scotian Shelf and Bay of Fundy, again deriving the insights from the extensive survey series (Scott 1988).

Throughout his career with DFO, Hamish applied his background in parasitology to the study of marine fish population structure, making numerous contributions to stock structure for various species, including pollock (*Pollachius virens*; Scott 1985), the five common species of hakes found on the Scotian Shelf (Scott 1987), Atlantic halibut (*Hippoglossus hippoglossus*), and Greenland halibut (*Reinhardtius hippoglossoides*; Scott and Bray 1989), haddock (*Melanogrammus aeglefinus*; Scott 1981) and Atlantic argentine (*A. silus*; Scott 1969).

Hamish demonstrated his creative and inquisitive nature by examining cod cleithra recovered from a shipwreck in 1865 and compared contemporary back-calculated cod sizes, as well as mercury and zinc content (Scott 1977).

Apart from his scientific contributions, Hamish made noteworthy contributions to science administration and leadership at the Biological Station. At the time of his retirement in the mid-1980s, Hamish was the Head of the St. Andrews component of the Marine Fish Division. In that capacity, Hamish provided calm and considered leadership during a tumultuous time in the 1970s, with the advent of extended jurisdiction of Canada's Exclusive Economic Zone (1977) and the division of mandate among federal government laboratories involved with Atlantic fisheries that resulted from integration of the old Fisheries Research Board laboratories with the Fisheries Department (R. Halliday, Fisheries and Oceans Canada, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, personal communication, 2010; P. Koeller, Fisheries and Oceans Canada, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, personal communication, 2010). Hamish also provided scientific mentorship through involvement in the supervisory committees of graduate students, particular those studying parasitology with Dr. M. Burt at the University of New Brunswick.

Hamish's careful work has been influential and no doubt will continue to be well-recognized. For example, his work on the depth, temperature, and salinity preferences of marine fish has been taken up by more recent investigations seeking to predict the impacts of climate change in the Northwest Atlantic (see, for example, Murawski 1993). His work on species assemblages and co-occurrences has also been considered ahead of its time and provided a foundation for advancing towards the goal of managing fisheries on an ecosystem basis (A. Bundy, Fisheries and Oceans Canada, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, personal communication, 2010).

His contributions to fisheries science and life at St. Andrews will always be appreciated.

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John D. Neilson
T. Derrick Iles
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St. Andrews, New Brunswick

HOMMAGE

J.S. Scott accueillant le Très Honorable Edward Schreyer lors de la visite du gouverneur général à la Station biologique de St. Andrews en 1983. P.A. Koeller apparaît en arrière plan.

James Stuart (Hamish) Scott (1924–2010)

Biologiste des pêches très productif et bien connu de la région Atlantique du Canada, Hamish Scott est décédé le 12 mars 2010 alors qu'il visitait sa ville natale de St. Andrews, Écosse.

Après avoir servi dans la Royal Navy durant la Seconde guerre mondiale, Hamish a terminé ses études de premier cycle à l'université St. Andrews avec spécialisation en géologie. Ses premières études académiques et ses prouesses lui ont valu d'être impliqué dans un inventaire important dans l'Himalaya népalais et ainsi de connaître deux des plus importants alpinistes de l'histoire : H.W. (Bill) Tilman (chef de l'expédition et écrivain) et le sherpa Tenzing Norgay, l'une des deux premières personnes à atteindre le sommet du mont Everest. L'inventaire consistait en une expédition exploratoire et scientifique de 4 mois dans les régions de Langtang, Ganesh et Jugal du Népal, au moment où ce pays commençait à s'ouvrir de nouveau aux étrangers.

Hamish s'est alors intéressé à l'écologie des populations de poissons. Durant un séjour de 10 années en Malaisie, il a travaillé pour le gouvernement colonial britannique et a publié une monographie sur les poissons marins de Malaisie (Scott 1959). Il a complété une thèse de doctorat en parasitologie à l'Université St. Andrews en 1963 (décrivant le développement post-embryonnaire de la larve du cestode *Paricterotaenia paradoxa*) et a travaillé pour le gouvernement britannique sur la mise en valeur des pêches commerciales au Nigéria pendant 3 ans. Il s'est ensuite établi avec sa famille à St. Andrews (Nouveau-Brunswick, Canada) à la fin de 1967 où a amorcé sa carrière à la Station biologique de St. Andrews.

Durant les années 1960, le travail de Hamish s'est concentré sur l'écologie classique des populations de poissons, y compris des études de méristique et de morphométrie, d'alimentation et de structure de population chez le merlu argenté (*Merlucius bilinearis*) et le lançon du nord (*Ammodytes dubius*; Scott 1968). Il a aussi contribué à la connaissance de la grande argentine (*Argentina silus*) par la description de plusieurs aspects du début de son cycle biologique. Durant cette période et la décennie qui a suivi, une partie importante des travaux de Hamish concernait les espèces qu'on considérait à l'époque comme sous-utilisées commercialement. C'est ainsi

que ses recherches ont contribué à combler un vide important dans les connaissances de la faune des poissons de la région canadienne du nord-ouest de l'Atlantique.

Durant la fin des années 1960 et le début des années 1970, Hamish et ses collègues de la Section des poissons de fond du ministère des Pêches et Océans (MPO) ont consenti des efforts considérables pour l'établissement d'inventaires aléatoires stratifiés en fonction de la profondeur des populations de poissons de fond de la plate-forme Néo-écossaise et de la baie de Fundy, dont les premiers furent réalisés en 1971. Ces inventaires annuels, conçus pour fournir des perspectives sur la répartition et l'abondance d'une gamme étendue d'espèces de poissons marins, continuent d'être une source indispensable de renseignements sur le statut de la faune des poissons de l'Atlantique canadien et sur leur milieux associés. Hamish a étendu ces inventaires aux eaux relativement peu profondes au large de l'île de Sable en 1980–1985, ce qui a comblé une des lacunes de ces inventaires (Scott 1982*b*).

Durant les années 1980, Hamish a démontré la valeur des inventaires en publiant les résultats sur les préférences de profondeur, température et salinité des poissons communs de la plate-forme Néo-écossaise (Scott 1982*a*) et la sélection du type de fond par les poissons benthiques (Scott 1982*c*), ainsi qu'en déterminant à l'aide d'analyses matricielles les occurrences conjointes saisonnières des espèces de poissons de fond sur la plate-forme Néo-écossaise (Scott 1989). Il a aussi produit avec d'autres chercheurs un rapport technique exhaustif et reconnu décrivant les répartitions spatiales saisonnières des poissons de fond de la plate-forme Néo-écossaise et de la baie de Fundy, dont les résultats principaux ont aussi été tirés des importantes séries d'inventaires (Scott 1988).

Au cours de sa carrière au MPO, Hamish a utilisé ses connaissances de base en parasitologie pour l'étude de la structure de population des poissons et a ainsi contribué à la détermination de la structure des stocks de nombreuses espèces, dont la goberge (*Pollachius virens*; Scott 1985), les cinq espèces communes de merluches vivant sur la plate-forme Néo-écossaise (Scott 1987), les flétans atlantique (*Hippoglossus hippoglossus*) et du Groenland (*Reinhardtius hippoglossoides*; Scott et Bray 1989), l'aiglefin (*Melanogrammus aeglefinus*; Scott 1981) et la grande argentine (*A. silus*; Scott 1969).

Hamis a fait preuve de créativité et d'ingéniosité lorsqu'il a examiné des cleithrums de morues récoltés dans une épave de 1865 et déterminé par rétro-calcul les tailles des morues ainsi que leur contenu en mercure et en zinc (Scott 1977).

En plus de ses contributions à la science, Hamish a fait montre de ses qualités de chef et de gestionnaire à la Station biologique. Au moment de sa retraite au milieu des années 1980, Hamish était le directeur de la composante de St. Andrews de la section des poissons marins. À ce titre, Hamish a présidé avec calme et sagesse à la période mouvementée dans les années 1970 qui a vu l'extension de la zone économique exclusive du Canada (1977) et la répartition des mandats entre les laboratoires du gouvernement fédéral impliquées dans les pêches atlantiques à la suite de l'intégration des laboratoires de l'ancien Conseil de recherche sur les pêcheries à ceux du ministère des Pêcheries (R. Halliday, Pêches et Océans Canada, Institut océanographique de Bedford, Dartmouth, Nouvelle-Écosse, communication personnelle, 2010; P. Koeller, Pêches et Océans Canada, Institut océanographique de Bedford, Dartmouth, Nouvelle-Écosse, communication personnelle, 2010). Hamish a aussi contribué à la direction scientifique d'étudiants de cycles supérieurs en s'impliquant dans leurs comités conseils, particulièrement les étudiants de parasitologie du Prof. M. Burt de l'Université du Nouveau-Brunswick.

Les travaux de haute qualité de Hamish ont eu une grande répercussion et continueront certainement à être hautement reconnus. Ainsi, ses recherches sur les préférences de profondeur, température et salinité des poissons marins sont utilisés dans des projets plus récents qui visent à prédire les effets du changement climatique dans le nord-ouest de l'Atlantique (voir, par exemple, Murawski 1993). Ses travaux sur les peuplements de poissons et leurs co-occurrences ont aussi été considérés comme innovateurs et ont servi de base pour la gestion des pêches en fonction des écosystèmes (A. Bundy, Pêches et Océans Canada, Institut océanographique de Bedford, Dartmouth, Nouvelle-Écosse, communication personnelle, 2010).

Ses contributions à la science de la pêche et à la vie à St. Andrews seront toujours très appréciées.

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Rates and components of carbon turnover in fish muscle: insights from bioenergetics models and a whole-lake ^{13}C addition

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Abstract: Stable isotopes are widely employed to describe energy flow in aquatic communities, though interpretation of results can be confounded by the fact that organisms integrate over vastly different time scales. We used results from a 56-day whole-lake ^{13}C addition and a bioenergetic modeling approach to estimate dorsal muscle carbon turnover rates in a natural setting for three sizes of bluegill (*Lepomis macrochirus*), largemouth bass (*Micropterus salmoides*), and yellow perch (*Perca flavescens*). Generally, dynamic $\delta^{13}C$ models with a metabolic tissue replacement term were better supported than models predicting isotopic change from growth alone, except when relative growth rates were highest (age 0 bluegill). Across species and size classes, the percentage of carbon change due to tissue replacement was variable (2%–80%) and independent of fish size. The half-life of $\delta^{13}C$ in age 0 fishes was similar and ranged from 8 to 18 days. In contrast, adult tissue half-lives were much longer (116–173 days). Based on these and previously published estimates, fish mass (g) was a strong predictor of fish carbon turnover rates, λ: $\log(\lambda) = -3.65 - 0.20\log(\text{mass})$, $r^2 = 0.71$.

Résumé : Les isotopes stables servent couramment à décrire le flux d'énergie dans les communautés aquatiques, même si le fait que les divers organismes les intègrent à des échelles temporelles extrêmement différentes peut introduire de la confusion dans l'interprétation des résultats. Nous utilisons une addition expérimentale de ^{13}C de 56 jours dans un lac entier et une méthodologie de modélisation bioénergétique pour estimer dans un environnement naturel les taux de remplacement du carbone dans le muscle dorsal chez trois tailles de crapets arlequins (*Lepomis macrochirus*), d'achigans à grande bouche (*Micropterus salmoides*) et de perchaudes (*Perca flavescens*). En général, les modèles dynamiques de $\delta^{13}C$ avec un terme de remplacement métabolique des tissus fonctionnent mieux que les modèles qui prédisent les changements isotopiques à partir de la seule croissance, sauf lorsque les taux de croissance relative sont à leur maximum (les crapets arlequins d'âge 0). Le pourcentage de changement de carbone dû au remplacement des tissus est variable (2–80 %) et indépendant de la taille des poissons chez les différentes espèces et les classes de taille. La demi-vie de $\delta^{13}C$ est semblable chez tous les poissons d'âge 0 et varie de 8–18 jours. En revanche, les demi-vies dans les tissus adultes sont beaucoup plus longues (116–173 jours). D'après les présentes estimations et d'autres publiées antérieurement, la masse du poisson (g) est une bonne variable prédictive des taux de remplacement du carbone (λ) chez les poissons: $\log(\lambda) = -3{,}65 - 0{,}20\log(\text{masse})$, $r^2 = 0{,}71$.

[Traduit par la Rédaction]

Introduction

The relationship between carbon stable isotopes in fish tissues and their diets has proven a valuable tool for tracing energy flow in food webs (DeNiro and Epstein 1978; Peterson and Fry 1987). The $\delta^{13}C$ of a fish's tissue conservatively reflects the $\delta^{13}C$ of its diet over longer time periods than direct measurements such as stomach content analysis (Vander Zanden et al. 1997). These properties facilitate tracing energy across multiple trophic levels, such as identifying primary production sources supporting fish growth (Forsberg et al. 1993). However, uncertainty about the length of time that tissues reflect diet $\delta^{13}C$ can cause doubt whether observed $\delta^{13}C$ differences owe to changes in trophic pathways or simply shifts in dietary $\delta^{13}C$ that are not completely reflected in tissue $\delta^{13}C$ (O'Reilly et al. 2002). Understanding how this dynamic value varies across common gradients, such as fish size, would facilitate ecological inference and increase the utility of stable isotopes for quantifying energy flow in aquatic food webs (Martínez del Rio et al. 2009).

The rate of carbon isotope turnover (λ) in an organism or tissue results from the addition of new tissue and metabolic replacement of existing tissue. To date, many fish $\delta^{13}C$ diet-switch studies concluded growth was primarily responsible for $\delta^{13}C$ change, and metabolic replacement had a negligible effect on turnover, but noted that results may not be consistent across all fish life stages (Hesslein et al. 1993; Herzka and Holt 2000; Perga and Gerdeaux 2005). Experiments on older or larger fishes and those with lower specific growth

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rates found replacement to be a major proportion of total turnover, in some cases accounting for 80% of isotopic change in dorsal muscle tissue (Suzuki et al. 2005; Tarboush et al. 2006; Logan et al. 2006). Knowledge of the principal factors that influence the relative importance of tissue replacement and growth in isotopic change would provide a mechanistic basis for predicting dynamics of $\delta^{13}C$ change in fishes (Martínez del Rio et al. 2009).

The relationship between rates of carbon isotope change and simple allometric and physiologic metrics, such as body size or temperature, remains poorly understood. In similar-sized fishes, higher water temperature reduced the half-life of carbon in muscle tissue (Bosley et al. 2002; Witting et al. 2004), supporting speculations by Tieszen et al. (1983) that metabolic activity is positively correlated with λ. The evidence for the negative relationship between body mass and turnover is consistent across studies. The isotopic half-life of larval fishes typically ranges from days to weeks and increases to months in larger fishes (Hesslein et al. 1993; MacAvoy et al. 2001), although many estimates on larger fishes are poorly constrained. Part of our knowledge gap on carbon turnover in fishes may simply owe to logistical laboratory constraints of conducting diet-switch experiments on larger individuals.

A lack of diversity in analytical approaches may also limit our understanding of how common factors, such as growth and size, influence isotopic change in fishes. Standard isotopic diet-switch experiments conducted in laboratory settings have been critical in providing isotopic rates of change, yet such studies most often use early life stages individuals, held under ideal temperatures for growth with ad libitum food sources. Such experiments offer the benefit of controlled conditions but have a harder time mimicking natural systems where fish incur metabolic costs associated with searching for food and predator avoidance. A few studies have estimated rates of isotopic change in natural settings by taking advantage of predictable changes in the isotopic value of fish diets associated with larval development or migration. (Vander Zanden et al. 1998; Maruyama et al. 2001). These studies more accurately reflect natural conditions experienced by fishes, but require a known, unidirectional change in diet isotopic value and usually assume exponential fish growth. An alternative approach to estimating isotopic rates of change uses daily fish growth and consumption estimates from bioenergetic models paired with isotopic time series of fish tissue and diet (Harvey et al. 2002). In contrast with the exponential models used by most isotopic turnover studies, this flexible method does not require a static change in the isotopic value of the diet and can account for temporal variation in fish growth rates owing to temperature or food quality. While not widely applied, this approach has the potential for estimating rates of isotopic change under a range of natural conditions.

We took advantage of an experimental, whole-lake ^{13}C addition to estimate carbon isotope ($\delta^{13}C$) turnover rates (λ) over a broad range of sizes (0.06–434 g) of three common north-temperate fishes. The experiment's original intent was to determine the relative importance of lacustrine and terrestrial energy sources supporting lake food webs. The added ^{13}C, in the form of sodium bicarbonate, drastically increased the $\delta^{13}C$ of primary production and created a contrast between the $\delta^{13}C$ of invertebrates consumed by fish and fish muscle tissue $\delta^{13}C$. We developed a simple mass balance model using bioenergetic-derived growth dynamics to estimate carbon isotope change rates in a natural setting, across a range of fish sizes and species. Using fish tissue and diet $\delta^{13}C$ time series, we evaluated the importance of growth and tissue replacement (m) to isotopic change by comparing models where m was equal to zero (isotopic change due to growth only) and where m was a constant proportion over the season. We combined our results with previously published carbon isotope change studies to evaluate and establish relationships among λ, fish size, and water temperature.

Materials and methods

The ^{13}C addition was conducted in Crampton Lake, which is located in a forested watershed of the University of Notre Dame Environmental Research Center (46°13′N, 89°32′W) in Michigan's Upper Peninsula. This oligotrophic 26 ha lake has a maximum depth of 18.5 m and a mean depth of 3.5 m. Bluegill (*Lepomis macrochirus*), largemouth bass (*Micropterus salmoides*), and yellow perch (*Perca flavescens*) dominate the fish community (>95% biomass), with less abundant populations of pumpkinseed (*Lepomis gibbosus*), johnny darter (*Etheostoma nigrum*), golden shiner (*Notemigonus crysoleucas*), and central mudminnow (*Umbra limi*). The lake shore is not developed, and the lake receives limited angling pressure and no harvest. We added ^{13}C in the form of sodium bicarbonate ($NaH^{13}CO_3$, >99% ^{13}C content) to the lake's upper mixed layer each morning (0700 h) for 56 days from 13 June to 7 August 2005. The $NaH^{13}CO_3$ was dissolved in gas-tight carboys filled with lake water, then pumped directly into the lake from a moving boat at a depth of 0.7 m while the boat traveled in a path that covered the entire lake area. This practice promoted dispersions throughout the mixed layer (Pace et al. 2007). Lake water temperature was measured every hour at 1.5 m using three HOBO Pendant data loggers deployed in different areas of the littoral zone. The daily average of these three measurements was used in bioenergetics models.

Sampling and measurement of $\delta^{13}C$, diet, and growth

Fish collections for muscle tissue $\delta^{13}C$ and diet were made every 5–14 days using angling and boat electrofishing. Bluegill (ages 0 and 2), largemouth bass (ages 0, 1, and 6), and yellow perch (ages 0 and 1) were collected from late May through the beginning of November 2005. Age 5 bluegill and age 2 yellow perch were sampled through 8 October 2005. Additional diet samples were collected from age 2 bluegill, age 1 yellow perch, and age 0 largemouth bass from early May through June 2006 to supplement the early season diet descriptions for these age classes. The particular species and age classes were chosen based on our ability to consistently sample within an age class and to represent a broad ontogenetic range in each species. We also used a purse seine in the deepest portion of the lake during June–August 2005 to capture age 0 yellow perch and bluegill that were not present in littoral areas during midsummer. Purse seines did not capture any larger fishes. Dorsal muscle tissue was dissected from individual fish (n = 1–5) in each species and age class, cleaned of scales and skin, rinsed with deion-

ized water, dried at 60 °C for 72 h, and homogenized. Isotope analyses of fish tissue were performed on isotope ratio mass spectrometers at the University of California – Davis stable isotope laboratory. The $\delta^{13}C$ data are reported in per mil (‰) notation relative to Pee Dee Belemnite.

We used gastric lavage, within 30 min of capture, to collect diets from fish greater than 80 mm total length. Contents were flushed into mesh-lined funnels (153 μm) and thoroughly rinsed with deionized water to ensure ^{13}C-labelled lake water did not contaminate diet samples. Smaller fish were euthanized with an overdose of MS-222, stored on ice, and stomachs were dissected in the laboratory. Diet collections were made during three time periods (0600–0800, 1300–1500, 1900–2100) to account for potential diel diet variability. The number of samples that characterized the weekly diet of each species and age class ranged from 4 to 104 per week (average 13.5). We quantified individual fish diets by dry mass proportion for each of 25 diet taxa. Benthic diet classifications included Amphipoda, Decapoda, Diptera, Ephemeroptera, Gastropoda, Hirundinea, Lepidoptera, Megaloptera, Odonata, Trichoptera, and Veneroida. Pelagic taxa consisted of *Chaoborus* sp., Cladocera (large and small), and Copepoda. Terrestrial prey consisted of invertebrates and vertebrates (Rodentia). Prey fish, bluegill, yellow perch, largemouth bass, and johnny darter (*E. nigrum*) were identified to species and categorized as young of year (YOY) or age 1+. Intact diet items were separated, counted, dried at 60 °C for 72 h, and weighed to the nearest milligram. For partially digested or masticated items, unique body parts were counted and dry mass was extrapolated using the average dry mass of a diet taxon calculated from dried, whole items.

The $\delta^{13}C$ of fish diet items was determined using freshly consumed, whole invertebrates from fish diet samples, benthic invertebrates collected directly from the lake substrate, and oblique zooplankton tows. Invertebrate samples collected from fish stomachs consisted of whole diet items from a given date. Diet-collected samples were thoroughly rinsed with deionized water to reduce contamination from other diet contents, combined, dried at 60 °C for 72 h, and homogenized. We measured the $\delta^{13}C$ of Odonata and Diptera from benthic grab samples collected during the ^{13}C addition (Solomon et al. 2008). Samples for zooplankton and *Chaoborus* sp. $\delta^{13}C$ were collected weekly using oblique net hauls in the upper mixed layer. Individual invertebrate taxa were separated under a dissecting microscope, dried, and homogenized (Pace et al. 2007). We did not explicitly measure the $\delta^{13}C$ of *Bosmina* sp. and *Chydorus* sp. but assumed the $\delta^{13}C$ time series of primary producers from Pace et al. (2007) approximated the $\delta^{13}C$ for these small zooplankton. Johnny darters were rare in fish diets, and we did not explicitly measure their $\delta^{13}C$. We assumed the age 1 yellow perch samples approximated the $\delta^{13}C$ of these small, benthic-oriented fishes. Isotope analyses of invertebrates were performed at the University of California – Davis stable isotope laboratory (Davis, California).

Annual growth during 2005 for each species and age class was estimated from transverse-sectioned sagittae otoliths collected from fishes during May and June 2006. Otoliths were mounted in epoxy, and a transverse section (~200 μm) was cut using a low-speed saw. Interpreted annuli were measured along a radius centered at the origin and oriented perpendicular to annual growth marks. The change in length of an individual fish was estimated from the last annual growth increment (2005) using the direct-proportion back-calculation method (Schramm et al. 1992). The change in biomass for each fish was calculated from species-specific length–weight relationships developed over the course of the study. We used the average change in biomass for each species and age class to represent growth in the bioenergetics models. Age 0 fishes recruited to our sampling gear in the middle of the summer. We used the average weight of 20 or more individuals, from the date of first capture, to represent the starting weight in age 0 bioenergetic models.

Model methods

In this study, fish diet $\delta^{13}C$ and fish growth rate were dynamic, rather than static as in most stable isotope diet-switch experiments. Because these values were changing over the course of the study, we could not use an exponential model to estimate λ. Instead, we used a bioenergetic-based growth model and measurements of fish diet $\delta^{13}C$ to predict fish muscle $\delta^{13}C$. We compared our estimated $\delta^{13}C$ time series with observed time series of dorsal muscle tissue $\delta^{13}C$ and compared models with and without metabolic replacement parameter (m) that increased the rate at which the fish reflect the $\delta^{13}C$ of their diet.

Bioenergetics models partitioned the measured annual growth into daily growth estimates and estimated taxon-specific consumption for each fish species and age class (Table 1). Bioenergetics model inputs included the average mass change over the season as estimated from otolith back-calculations, measured weekly diet proportions, literature values for predator and prey energy densities, and the daily mean water temperature at 1.5 m. We used previously published bioenergetics model parameters for bluegill (Kitchell et al. 1974), largemouth bass (Rice et al. 1983), and yellow perch (age 1, age 2 — Kitchell et al. 1977; age 0 — Post 1990). We assumed predator and prey energy densities were constant over time and obtained values from the literature (Cummins and Wuycheck 1971) and those included in Hanson et al. (1997). We used the carbon to nitrogen ratio (C:N), from stable isotope analysis, to assess our assumed energy density temporal consistency within a prey category and to corroborate the magnitude of differences in literature-based energy densities among prey. We included spawning losses of 15% of wet mass in age 5 bluegill and age 6 largemouth bass bioenergetics models (Kitchell et al. 1974; Rice et al. 1983). Bioenergetics models were run at a daily time step from 19 May 2005 through 25 October 2005 for all age classes except YOY, which started on the first day of capture, 17 July 2005, 9 July 2005, and 27 June 2005 for bluegill, largemouth bass, and yellow perch, respectively (Table 1).

Fish diet $\delta^{13}C$ was calculated as a weighted average using observed diet taxa $\delta^{13}C$ time series and bioenergetics estimates of daily taxon-specific consumption. Fish's diet $\delta^{13}C$ was calculated each day according to

$$\text{(1)} \quad \text{DIET } \delta^{13}C_{(t)} = \frac{\sum_j \left(\delta^{13}C_{j(t)} \cdot Q_{j(t)}\right)}{Q_{(t)}}$$

Table 1. Species- and age-specific sample sizes for diet and growth characterization, bioenergetics models start masses, end masses, model duration, estimated proportion of maximum consumption, and citation for bioenergetics model parameters.

Species	Age	Diet (*N*)	Growth (*N*)	Mass start (g)	Mass end (g)	Model duration	Prop. max. consump.	Bioenergetics model
Bluegill	0	102	18	0.06	1.20	17 July – 4 Nov.	0.86	Kitchell et al. 1974
	2	278	21	5.38	15.97	19 May – 4 Nov.	0.52	Kitchell et al. 1974
	5	407	11	72.70	108.60	19 May – 8 Oct.	0.53	Kitchell et al. 1974
Largemouth bass	0	55	25	0.52	4.60	9 July – 4 Nov.	0.59	Rice et al. 1983
	1	177	27	5.60	42.60	19 May – 4 Nov.	0.45	Rice et al. 1983
	6	400	14	413.00	474.00	19 May – 4 Nov.	0.26	Rice et al. 1983
Yellow perch	0	110	10	0.11	2.60	27 June – 4 Nov.	0.49	Post 1990
	1	161	23	2.24	9.13	19 May – 4 Nov.	0.39	Kitchell et al. 1977
	2	56	8	11.16	17.32	19 May – 8 Oct.	0.32	Kitchell et al. 1977

where $\delta^{13}C_{j(t)}$ is the $\delta^{13}C$ of diet item j, consumed on day t, $Q_{j(t)}$ represents the daily mass of diet item j, consumed on day t, and $Q_{(t)}$ is the total mass consumed on day t. $\delta^{13}C_{j(t)}$ was derived from observed or linearly interpolated diet item $\delta^{13}C$ throughout the experiment. For days that we did not measure diet item $\delta^{13}C$, we linearly approximated values between single $\delta^{13}C$ measurements or the average $\delta^{13}C$ if more than one sample was analyzed from a given day.

The $\delta^{13}C$ of the fish on day $t + 1$ is predicted from a mass-weighted mixing equation for $\delta^{13}C$ ($\delta^{13}C$ mass at time $t + 1$ is equal to $\delta^{13}C$ mass carried over from time t + $\delta^{13}C$ mass in growth during the time interval plus the ^{13}C mass in tissue replacement during the time interval)

$$\text{(2a)}\quad \delta^{13}C_{fish(t+1)} \cdot M_{(t+1)} = \delta^{13}C_{fish(t)} \cdot [(1-m) \cdot M_{(t)} \cdot \Delta_t] + \left(\delta^{13}C_{diet(t)} + D\right) \cdot G_{(t)} + \left(\delta^{13}C_{diet(t)} + D\right) \cdot m \cdot M_{(t)} \cdot \Delta_t$$

which gives the following expression for $\delta^{13}C_{fish(t+1)}$:

$$\text{(2b)}\quad \delta^{13}C_{fish(t+1)} = \frac{\delta^{13}C_{fish(t)} \cdot [(1-m) \cdot M_{(t)} \cdot \Delta_t] + \left(\delta^{13}C_{diet(t)} + D\right)\left(G_{(t)} + m \cdot M_{(t)} \cdot \Delta_t\right)}{M_{(t+1)}}$$

In eqs. 2*a* and 2*b*, $\delta^{13}C_{fish(t)}$ is the calculated fish $\delta^{13}C$, $M_{(t)}$ is the fish mass on day t, and $M_{(t+1)}$ is the fish mass on day $t + 1$. The values for $G_{(t)}$, $M_{(t)}$, and $M_{(t+1)}$ are based on the species- and age-specific bioenergetics models described above. More specifically, $G_{(t)}$ represents fish growth (in grams) at time t, and $M_{(t)}$ and $M_{(t+1)}$ represent fish mass (g) at time t and $t + 1$, respectively. $\delta^{13}C_{diet(t)} + D$ (discrimination factor between diet and muscle tissue) represents the $\delta^{13}C$ of newly added tissue and replaced tissue, and the initial fish $\delta^{13}C_{fish}$ is the mean of $\delta^{13}C$ measurements on the first day tissue samples were analyzed. We use the term "discrimination factor", as proposed by Martínez del Rio et al. (2009), to describe the difference in the isotopic composition between an animal's tissue and its diet. We assumed a $\delta^{13}C$ discrimination factor between diet and fish dorsal muscle tissue of 0.80 (Vander Zanden and Rasmussen 2001). The parameter m is proportion of fish mass that is turned over via metabolic replacement each day, and Δ_t is the time step in days ($\Delta_t = 1$ day) over which the model is evaluated. To determine if metabolic tissue replacement was important in the rate of isotopic change, we compared models where metabolic replacement (m) was either zero (growth only) or constant through time using the Akaike information criterion (AIC) for least squares (Burnham and Anderson 1998). We calculated the uncertainty in our estimates of m by bootstrapping model residuals ($\delta^{13}C_{observed} - \delta^{13}C_{predicted}$). For each bootstrap iteration, we resampled the vector of residuals with replacement, we added the resampled error to each fish tissue $\delta^{13}C$ observation in the time series, and we refit the model (eq. 2) to create a distribution of m estimates (Efron and Tibshirani 1993). Uncertainty in m is represented as the standard deviation of these 1000 estimates. All analyses were performed with the R statistical package (R Development Core Team 2008).

To compare our rates of isotope change to other studies, we calculated a single rate of carbon isotope change (λ) that includes the effects of growth and metabolic replacement by simulating tissue $\delta^{13}C$ over a static $\delta^{13}C$ diet switch. We assumed a fish started in equilibrium with its diet at a $\delta^{13}C$ of −25‰ and was switched to a constant diet with a $\delta^{13}C$ of −15‰. For a given species and age, simulations followed the bioenergetic starting masses, growth trajectories, and time periods listed in Table 1. We calculated fish tissue $\delta^{13}C$ with eq. 2, using bioenergetic daily growth estimates, the fitted metabolic replacement parameter (m), and a constant diet of −15‰. We then fit the single-compartment, time-based expo-

nential model of Martínez del Rio and Wolf (2005) to the simulated fish $\delta^{13}C$ estimates. The model was

$$(3) \quad \delta X_{\text{tissue}(t)} = \delta X_{\infty} - \left(\delta X_{\infty} - \delta X_{\text{tissue}(0)}\right)e^{-\lambda t}$$

where $\delta X_{\text{tissue}(t)}$ is the $\delta^{13}C$ at time t, δX_{∞} is the isotopic value of the tissue in equilibrium with its new diet, $\delta X_{\text{tissue}(0)}$ is the isotopic value of the tissue prior to the diet switch, and λ is isotopic turnover, which includes the combined effects of growth and metabolic replacement. We fit λ by minimizing the sum of squares using optimization routines in the R statistical package (R Development Core Team 2008). The half-life of carbon in dorsal muscle was calculated as

$$(4) \quad \text{half} - \text{life} = \frac{\ln(2)}{\lambda}$$

where half-life is represented in days. In these simulations, daily growth followed bioenergetic model estimates, rather than assuming a single exponential growth rate as in many isotope change studies where fish are grown at a single temperature and ration. Accordingly, we could not partition λ into single rates of isotopic change due to growth and metabolic replacement. Instead, we separately summed the daily mass contributions of growth and replacement for each of the 1000 bootstrap iterations (eq. 2). We report the proportional importance of growth and replacement to isotopic change as the mean and standard deviation of these 1000 proportions.

We combined our estimates of λ with those from the literature to determine the relationship among fish size, water temperature, and λ. We restricted our literature search to studies that reported some measure of fish size, water temperature, and λ. For each study or different experimental condition, we used the single reported water temperature, the reported mean temperature, or modal water temperature if a range was given. Fish mass was represented by a single fish mass or a mean mass at the beginning of an experiment. Martínez del Rio et al. (2009), using relationships from Gillooly et al. (2001), proposed that an animal's isotopic incorporation rate should relate to individual mass and temperature-regulated metabolic rate as

$$(5) \quad \lambda \sim m_b^{-\frac{1}{4}} \cdot e^{\frac{-E_a}{kT}}$$

where m_b is fish mass, E_a is the energy of activation of metabolic processes (constant), k is the Boltzmann's constant, and T is temperature (in Kelvin). We evaluated the influences of fish size and temperature using a simplified form of eq. 5, where the natural log of λ is a function of the natural log of mass, where logλ is a function of mass and is temperature represented as an Arrhenius exponential (T^{-1}), or where logλ is a function of mass and temperature is represented with an exponential approximation (T). We compared models using AIC for least squares (Burnham and Anderson 1998).

Results

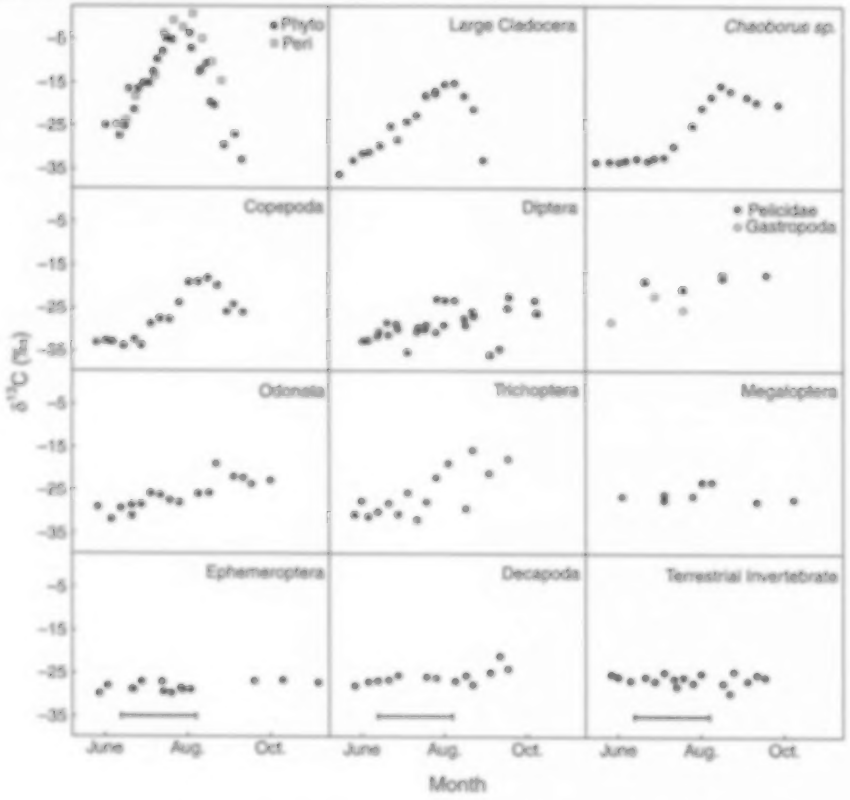
The added sodium bicarbonate (>99% ^{13}C content) elevated the lake water dissolved inorganic carbon $\delta^{13}C$ from an initial value of approximately −12‰ to 5‰–15‰. The $\delta^{13}C$ of both pelagic and benthic primary production rapidly increased 20‰–30‰ during the ^{13}C addition and returned to pre-addition $\delta^{13}C$ levels shortly after the addition ended (Pace et al. 2007). We observed large, consistent increases in zooplankton $\delta^{13}C$ (15‰–20‰), while benthic invertebrate $\delta^{13}C$ increases were less extreme and more variable among groups (0‰–13‰, Fig. 1). The $\delta^{13}C$ of terrestrial diet taxa did not increase over the course of the addition (mean = −26.4‰, 1 SD = 1.2‰; Fig. 1). Increases in invertebrate $\delta^{13}C$ resulted in fish diet $\delta^{13}C$ increases of 10‰–15‰ (Fig. 2).

Of the 25 taxa used to describe the fish diets, six or fewer diet categories represented most of the taxon-specific consumption estimates for any species or age class. Diets of age 2 and age 5 bluegill were chiefly composed of Trichoptera, Odonata, Diptera, and terrestrial invertebrates, while age 0 bluegill consumed small Cladocera (*Bosmina* sp. and *Chydorus* sp.), Trichoptera, and Diptera (Table 2). Ages 1 and 2 yellow perch diets were less diverse, consuming Odonata, Trichoptera, Diptera, and age 0 bluegill (Table 2). Age 0 yellow perch and largemouth bass consumed small Cladocera throughout the season, as well as Odonata and Diptera larvae (Table 2). Age 0 and age 1 yellow perch and bluegill were the primary components in both age 1 and age 6 largemouth bass diets (Table 2). Supplementary diet samples collected in May and June 2006 for juvenile fishes were similar to those collected in 2005 (same taxa) and consisted primarily of small benthic invertebrates (Trichoptera and Diptera) and small Cladocera (*Bosmina* sp. and *Chydorus* sp). We found no linear relationship in the C:N ratio for any of the 16 prey categories for which we had three or more samples of percent carbon and nitrogen ($0.06 < p < 0.75$). Across taxa, our assumed prey energy densities were negatively correlated with the average prey C:N ratio ($p < 0.01$).

The model that included the metabolic replacement parameter m had a lower AIC than the growth-only model for each species and age class, except age 0 bluegill (Table 3). Support for including m in the yellow perch models was weak, as indicated by small differences between model AIC values (0.4–2.4). We report goodness of fit statistics and estimated model parameters for all the models including metabolic replacement (Table 4). Standard errors of model residuals ranged from 0.27‰ to 0.90‰ and were substantially smaller than the observed increases in fish tissue $\delta^{13}C$ (5‰–20‰, Table 3). Estimates for λ ranged from 0.0060 to 0.0840 g·g^{-1}·day^{-1} and were negatively associated with fish size (Table 4). The exponential model accurately fit the simulated diet-switch data for all species and age classes and yielded half-life estimates that ranged from 8 days for age 0 yellow perch to 173 days for age 6 largemouth bass (Table 4). In our simulations, the proportional importance of growth (0.21–0.96) and metabolic replacement (0.02–0.79) in contributing to overall isotopic change was variable and was not associated with size.

We combined our isotopic change results with those of 13 previously published studies that reported some measure of fish size and water temperature. We excluded one lambda value (0.0006) from Sweeting et al. (2005) as an outlier, given it was sevenfold smaller than the next smallest lambda value that we considered. There was a strong negative relationship between λ and fish mass (Fig. 3; Table 5). Includ-

Fig. 1. $\delta^{13}C$ time series of primary producers (upper left panel; solid squares, phytoplankton; open squares, periphyton) and invertebrate taxa (solid and open circles, all other panels) during the experimental ^{13}C addition, Crampton Lake, 2005. Month labels on the *x* axis represent the first day of each month. The horizontal line above the *x* axis demarcates the timing of the ^{13}C addition. Primary producer $\delta^{13}C$ data, from Pace et al. (2007), is included for reference to secondary consumers and as a proxy for $\delta^{13}C$ of *Bosmina* sp. and *Chydorus* sp. Diptera and Odonata $\delta^{13}C$ data are from both Solomon et al. (2008) and invertebrates collected from fish diets. All other invertebrate samples were collected from fish diets in this study.



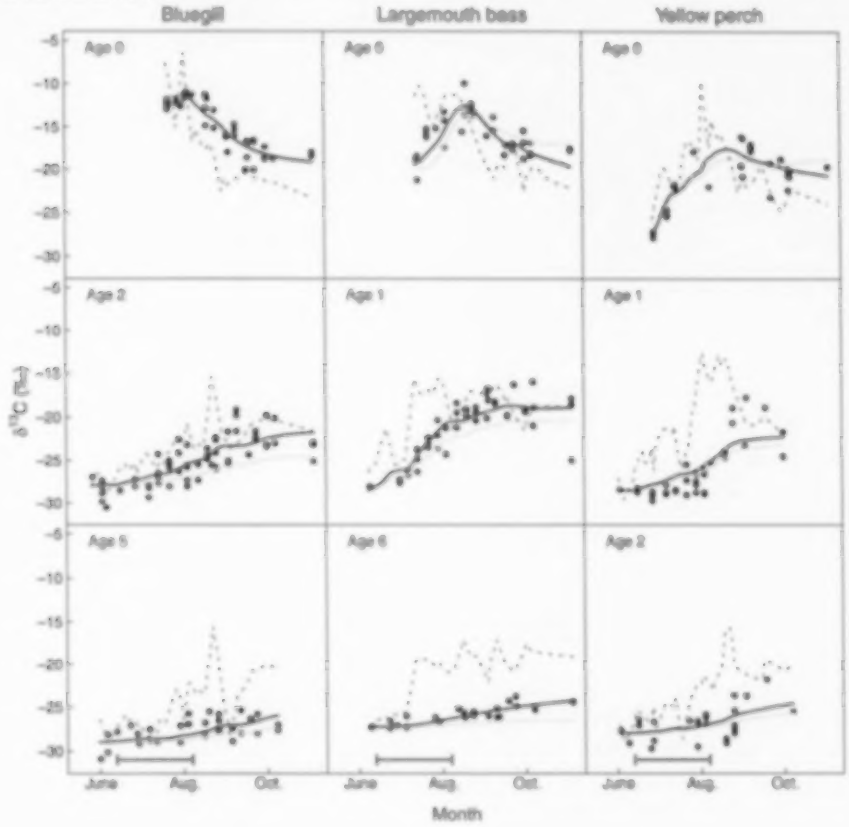
ing water temperature or the inverse of water temperature as an additional explanatory variable did not significantly improve the prediction of turnover rate based on AIC (Table 6).

Discussion

We found that models including a tissue replacement parameter were generally better supported by the $\delta^{13}C$ data than models predicting carbon turnover based solely on growth. There was only weak support for the replacement term in yellow perch, where model AIC values differed by less than 2.5. Our results are consistent with more recent isotopic turnover studies that found metabolic replacement can be a significant component of isotopic turnover (Suzuki et al. 2005; Logan et al. 2006; Tarboush et al. 2006). These conclusions are in contrast with studies that assert growth is the dominant factor influencing $\delta^{13}C$ change in fishes (Sakano et al. 2005; Perga and Gerdeaux 2005). The generalizations about what controls a fish's isotopic turnover rate based on early studies may have been biased by the sizes of organisms used and the conditions under which initial experiments were conducted (Tarboush et al. 2006). Early studies used juvenile fishes, with high growth/body size ratios, held in temperatures and conditions that were optimal for growth (Hesslein et al. 1993; Herzka and Holt 2000). Mass-specific growth rates are maximized in larval and juvenile stages, so studies on these life stages are likely a poor predictor of the relative importance of growth and metabolic replacement to isotopic turnover over the entire life of a fish, particularly older ages. While initial turnover studies concluded that the contribution of metabolic tissue replacement to isotopic turnover was small or negligible, some studies suggested this result may not be consistent in older, slower growing individuals (Fry and Arnold 1982).

The variable influence of tissue replacement in predicting age 0 fish $\delta^{13}C$ dynamics was unanticipated based on previous studies that concluded growth accounted for the majority of isotopic change in juvenile fishes (Vander Zanden et al. 1998; Sakano et al. 2005). Interspecific variability in the bioenergetics model parameter that represents the proportion of maximum consumption (*p* value) may explain differences in the importance of replacement in age 0 fishes. This bioenergetics parameter can be difficult to quantify. It is influenced by a range of physiological factors such as activity and ration quality. A *p* value of 1.0 represents maxi-

Fig. 2. Observed and model-predicted $\delta^{13}C$ values for different age classes of largemouth bass, bluegill, and yellow perch from Crampton Lake, 2005. Points represent dorsal muscle $\delta^{13}C$ observations. The broken line represents the diet $\delta^{13}C$. The solid black line is the model-predicted $\delta^{13}C$ including a term for metabolic tissue replacement. The solid grey line is the model-predicted $\delta^{13}C$ based on growth alone, without metabolic replacement. Month labels on the *x* axis represent the first day of each month. The horizontal line above the *x* axis demarcates the timing of the ^{13}C addition.



mum consumption for a given fish size and temperature. The age 0 bluegill *p* value was 0.88, suggesting bluegill growth over the 2005 season was near the maximum value for the given temperature conditions. Conversely, the *p* values for age 0 yellow perch ($p = 0.40$) and largemouth bass ($p = 0.57$) were much lower than that for bluegill. For both of these species, including the metabolic replacement term increased the model's support, although the support in yellow perch models was weak. Similarly, Witting et al. (2004) found evidence of tissue replacement in juvenile summer flounder with growth rates below their maximum rate (~60%), but lacked statistical power to include replacement as a significant predictor of isotope change. Our results suggest the relative importance of growth and metabolic turnover may be linked to growth efficiencies, where the rate of carbon isotope change is driven by growth when growth efficiencies are high and more related to metabolic rate when growth efficiencies are low. Future turnover studies, whether in natural or laboratory settings, would benefit from treatments that directly address how fish growth rate or growth efficiencies influence the proportional importance of metabolic replacement and growth in isotopic change.

The bioenergetics models provide a method to explicitly account for temperature, food and consumer energy densities, and size-specific physiology in isotopic change studies. This flexible approach may be useful in understanding how natural complexities that are difficult to simulate in laboratory conditions influence isotopic rates of change, including temporal variation and dependence on food abundance and quality (Martínez del Rio et al. 2009). The choice of appropriate bioenergetic model parameters is important and can influence analyses and interpretation that depend on these models of fish growth dynamics. For example, the bluegill and yellow perch bioenergetic models used have been shown to underestimate consumption by inaccurately accounting for fish activity costs (Rowan and Rasmussen 1996; Trudel and Rasmussen 2001). These underestimates of consumption would likely have had little influence on our rates of carbon isotope change, as fish diet proportions and annual growth would remain unchanged, and therefore the fish diet $\delta^{13}C$, which drive our model estimates of *m*, would likely not change appreciably. The bioenergetics models used in this study predict the growth pattern for the average fish and therefore cannot account for individual-

Table 2. Species- and age-specific diet composition by dry mass (percentage) for bluegill, yellow perch, and largemouth bass from Crampton Lake, 2005 and spring of 2006.

	Bluegill			Largemouth bass			Yellow perch		
Diet taxa	Age 0	Age 2	Age 5	Age 0	Age 1	Age 6	Age 0	Age 1	Age 2
Amphipoda		<1	3			<1		3	3
Bluegill, YOY		<1	4	30	12	11		7	5
Bluegill, age 1+						12			
Chaoborus sp.		<1	5	2					
Cladocera, large	26	8	5	21	3		37	18	<1
Cladocera, small	26	1	<1	7			15		<1
Copepoda	5	3	<1	16			15	<1	<1
Decapoda			2		1	10			4
Diptera	21	22	13	3	2	<1	7	11	9
Ephemeroptera		3	3		<1	1		1	4
Gastropoda			2			<1			
Hirundinea			2						
Johnny darter			1			8			
Largemouth bass, YOY					9	7		2	
Largemouth bass, age 1+						4			
Lepidoptera		<1	3						
Megaloptera	<1		3		<1	<1	2		
Odonata	4	18	16	3	12	2	12	49	53
Terrestrial vertebrate						2			
Terrestrial invertebrate	1	17	16	6	9	3		2	3
Trichoptera	17	25	18	2	3	1	11	5	11
Unidentifiable invertebrates			<1	1		<1			
Yellow perch, YOY			1	10	48	13		1	9
Yellow perch, age 1+					1	25		1	25
Veneroida		3	3		1			1	

Table 3. Sample sizes and Akaike information criterion (AIC) values for $\delta^{13}C$ time series models without a metabolic replacement term ($m = 0$) and where m is constant over time.

Species	Age	$\delta^{13}C$ (N)	$m = 0$, $p = 1$	m = constant, $p = 2$
Bluegill	0	36	9.5	11.2
	2	31	111.1	66.4
	5	36	23.6	16.9
Largemouth bass	0	29	53.2	38.4
	1	42	76.5	48.1
	6	25	16.1	−28.2
Yellow perch	0	25	36.8	34.4
	1	34	52.6	51.6
	2	25	28.4	28.0

Note: The number of penalized parameters (p) used in AIC calculations, including the error term, is noted under each model.

level variability in growth or diet. Additionally, our bioenergetic approach cannot statistically estimate separate rates of isotopic change due to growth and metabolic replacement. In contrast, isotope change studies that employ static diet $\delta^{13}C$ shifts and model growth exponentially or independently measure growth can statistically estimate the importance of these processes in influencing the isotopic change in fish tissue.

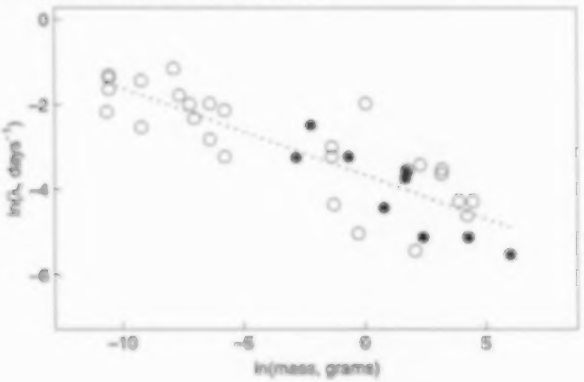
A number of important assumptions may influence our results. First, we did not mathematically correct for or extract lipids from fish tissue samples prior to analysis, although this likely had little effect because lipid content in muscle tissue of our study species is low. Post et al. (2007) concluded lipid correction is not necessary when tissue C:N ratio was <3.5; mean C:N ratios were 3.2, 3.5, and 3.6 for bluegill, yellow perch, and largemouth bass, respectively. Second, most studies of aquatic consumers assume a discrimination factor between diets and tissue of 0‰–1‰ (DeNiro and Epstein 1978). We chose to use a consistent discrimination factor of 0.80, which was the mean estimate from seven fish species (Vander Zanden and Rasmussen 2001). If the true isotopic shift between a fish tissue and diet in our study was closer to zero, our model estimates of half-life decrease on average by 12% (range: −33% to +3%). Conversely, if the isotopic shift is closer to 2.0‰ as suggested by Pinnegar and Polunin (1999) and Barnes et al. (2007), our half-life estimates increase by an average of +30%, although results are variable (range: 20% decrease to 100% increase). Similarly, a higher assumed discrimination factor increases the relative importance of metabolic replacement in isotopic change, while a discrimination factor of zero results in a greater proportion of change being attributed to growth. Well-constrained discrimination factor estimates are critically important for isotopic turnover studies that use dynamic models such as those in this study or for studies with larger individuals, because large fishes will rarely reach equilibrium with dietary $\delta^{13}C$. While bootstrapping provided an estimate for uncertainty around m, this certainly represents a lower bound estimate because we did not explicitly account for variability in growth, diet, diet item $\delta^{13}C$, or discrimination factor. Accounting for these additional sources of variability would not have ultimately

Table 4. Summary of species and age model results for the model that includes a constant tissue replacement (m).

Species	Age	m (SD)	Mean error (‰)	Growth (SD)	Replacement (SD)	λ (day^{-1})	Half-life (days)
Bluegill	0	0.0010 (0.0018)	0.27	0.96 (0.06)	0.02 (0.03)	0.0390	18
	2	0.0143 (0.0026)	0.43	0.32 (0.04)	0.68 (0.03)	0.0240	29
	5	0.0033 (0.0012)	0.27	0.43 (0.08)	0.57 (0.08)	0.0060	116
Largemouth bass	0	0.0228 (0.0058)	0.43	0.42 (0.06)	0.58 (0.06)	0.0395	18
	1	0.0121 (0.0027)	0.85	0.45 (0.09)	0.55 (0.06)	0.0280	25
	6	0.0031 (0.0003)	0.08	0.21 (0.02)	0.79 (0.02)	0.0040	173
Yellow perch	0	0.0131 (0.0076)	0.65	0.46 (0.17)	0.54 (0.17)	0.0840	8
	1	0.0026 (0.0014)	0.90	0.92 (0.10)	0.08 (0.10)	0.0120	58
	2	0.0029 (0.0010)	0.56	0.66 (0.17)	0.34 (0.17)	0.0060	116

Note: We report the fitted value for m, with bootstrapped error estimates, the mean error between observed and predicted δ^{13}C measurements (‰), and the proportion of isotopic change, by mass, due to growth and metabolic replacement processes. Standard deviations (SD) of m and the proportions of isotopic change due to growth and replacement were computed with 1000 bootstrap iterations. Additionally, we report the results of the simulated static diet switch, where λ represents the overall isotopic turnover rate, and dorsal muscle half-life is calculated as $\ln(2)/\lambda$.

Fig. 3. Fish dorsal muscle isotopic turnover is negatively related to fish size. The broken line ($\log(\lambda) \approx -3.65 - 0.20\log(\text{mass})$, $r^2 \approx 0.71$) represents the natural log relationship from both literature values (open circles) and values from this study (solid circles) as estimated by ordinary least squares. Note that the slope is similar to −0.25, which is the slope predicted by allometric and metabolic theory (Martínez del Rio et al. 2009).



changed our best estimates of m, but would likely increase our confidence bounds for this parameter.

The large δ^{13}C contrast between fish diets and fish tissue provided by the stable isotope addition was fundamental to estimating isotopic turnover rates in our study system. While isotope additions can be cost prohibitive at the ecosystem scale, researchers have taken advantage of changes in fish behavior and dietary δ^{13}C to estimate tissue turnover rates in natural systems. Such studies have included migration, rapid development, and seasonal diet changes (Vander Zanden et al. 1998; Maruyama et al. 2001; Perga and Gerdeaux 2005). Bioenergetics models offer an alternative analytical approach for understanding isotopic change in these natural settings.

The combination of frequent diet sampling and the ^{13}C addition identified a less traditional lake food web connection that was critical in predicting juvenile fish δ^{13}C dynamics. The δ^{13}C of age 0 bluegill and age 0 largemouth bass peaked at approximately −10‰, while the most enriched invertebrate food source we measured, pelagic zooplankton, only reached −16‰. Our results suggest these fishes did not rely on large Cladocera as their primary food source, but must have obtained energy from a source with higher δ^{13}C. Diet data revealed that small-bodied Cladocera, primarily *Bosmina* sp., were the dominant zooplankton found in age 0 fish diets, but these species were not abundant in pelagic zooplankton samples (Pace et al. 2007). Because we did not specifically measure the δ^{13}C of these small-bodied zooplankton taxa, we assumed the δ^{13}C of primary production approximated their carbon isotope value. This assumption is supported by the fast relative growth rates and small body size of *Bosmina* sp. compared with larger Cladocera (e.g., *Holopedium gibberium*, *Diaphanasoma bergei*) (Pennak 1978) and the fact that their midsummer abundance peak in lakes of this region coincided with the ^{13}C addition (Carpenter and Kitchell 1993). If the δ^{13}C of small-bodied Cladocera were more negative than we assumed, fish diet δ^{13}C would have been lower, and fish δ^{13}C time series models would have attributed a higher proportion of isotopic change to metabolic replacement. Subsequent investigations in Crampton Lake have recorded high densities (>1000 individuals per litre) of *Bosmina* sp. at total depths of 1–2 m. Together, these observations suggest that zooplankton heterogeneity between pelagic and nearshore habitats may play an important role in understanding carbon sources supporting fish. An alternative explanation for the high δ^{13}C values of age 0 fishes is that gape limitation of age 0 fishes restricted them to consume smaller benthic invertebrates, which may have had a higher δ^{13}C relative to larger conspecifics, but were underrepresented in pooled dietary δ^{13}C samples. The discrepancy between juvenile fish tissue δ^{13}C and measured prey δ^{13}C highlights the importance of dietary δ^{13}C information to our modeling approach. Future studies employing this approach may find it useful to directly analyze δ^{13}C from homogenized fish diets rather than separating diet items to be analyzed.

The long tissue half-lives of adult fishes in our study contradict the oft-held assumption of equilibrium between consumers and their diet (Gannes et al. 1997; Tarboush et al. 2006). Our result reinforces the need to consider the diet legacy incorporated into a point estimate for a tissue δ^{13}C value. This long period of incorporation means the small

Table 5. Previously published carbon turnover rates (λ), half-life, and experimental conditions for studies on fish muscle tissue and whole fish.

Species	λ (‰·day^{-1})	SD	Half-life (days)	Temp. (°C)	Mass (g)	Study
Red drum (*Sciaenops ocellatus*)	0.1150		6.0	28.00	2.40×10^{-5}	Herzka and Holt 2000*,†
	0.1380		5.0	28.00	7.40×10^{-4}	Herzka and Holt 2000*,†
	0.0990		7.0	24.00	8.90×10^{-4}	Herzka and Holt 2000*,†
Channel catfish (*Ictalurus punctatus*)	0.0140		49.5	15.00	8.67×10^{1}	MacAvoy et al. 2001
Winter flounder (*Pleuronectes americanus*)	0.1700	0.024	4.1	13.00	4.80×10^{-4}	Bosley et al. 2002*
	0.3200	0.038	2.2	18.00	3.80×10^{-4}	Bosley et al. 2002*
Pintado (*Pseudoplatystoma corruscans*)	0.0066		105.0	26.69	7.70×10^{-1}	Furuya et al. 2002
Japanese flounder (*Paralichthys olivaceus*)	0.1400		5.0	18.50	1.06×10^{0}	Tominaga et al. 2003
	0.0400		17.3	18.15	2.60×10^{-1}	Tominaga et al. 2003
	0.0500		13.9	17.00	2.60×10^{-1}	Tominaga et al. 2003
Summer flounder (*Paralichthys dentatus*)	0.0800	0.02	8.7	13.00	1.00×10^{-4}	Witting et al. 2004*
	0.2400	0.02	2.9	22.00	1.00×10^{-4}	Witting et al. 2004*
	0.0600	0.01	11.6	13.00	1.70×10^{-3}	Witting et al. 2004*
	0.1400	0.02	5.0	22.00	1.70×10^{-3}	Witting et al. 2004*
	0.0400	0.06	17.3	13.00	3.10×10^{-3}	Witting et al. 2004*
	0.1200	0.04	5.8	22.00	3.10×10^{-3}	Witting et al. 2004*
Japanese temperate bass (*Lateolabrax japonicus*)	0.0330		21.0	23.00	9.87×10^{0}	Suzuki et al. 2005
European sea bass (*Dicentrarchus labrax*)	0.0044		157.5	12.00	8.00×10^{0}	Sweeting et al. 2005
Nile tilapia (*Oreochromis niloticus*)	0.0297		23.3	25.00	2.446×10^{1}	Zuanon et al. 2006
	0.0267		26.0	25.00	2.378×10^{1}	Zuanon et al. 2006
Zebra danio (*Danio rerio*)	0.0130		53.3	28.50	2.80×10^{-1}	Tarboush et al. 2006
Sand goby (*Pomatoschistus minutus*)	0.0290	0.011	23.9	17.00	5.85×10^{0}	Guelinckx et al. 2007
Senegalese sole (*Solea senegalensis*)	0.2730		2.5	21.50	2.63×10^{-5}	Gamboa-Delgado et al. 2008*
	0.2560		2.7	21.50	2.63×10^{-5}	Gamboa-Delgado et al. 2008*
	0.1970		3.5	21.50	2.63×10^{-5}	Gamboa-Delgado et al. 2008*
Summer flounder (*Paralichthys dentatus*)	0.0101		69.0	19.90	5.88×10^{1}	Buchheister and Latour 2010
	0.0140		49.0	20.40	1.02×10^{2}	Buchheister and Latour 2010
Bluegill (*Lepomis macrochirus*)	0.0390	0.0018	18.0	21.50	6.00×10^{-2}	This study
	0.0240	0.0026	29.0	21.50	5.38×10^{0}	This study
	0.0060	0.0012	116.0	21.50	7.27×10^{1}	This study
Largemouth bass (*Micropterus salmoides*)	0.0395	0.0058	18.0	21.50	5.20×10^{-1}	This study
	0.0280	0.0027	25.0	21.50	5.60×10^{0}	This study
	0.0040	0.0003	173.0	21.50	4.13×10^{2}	This study
Yellow perch (*Perca flavescens*)	0.0840	0.0076	8.0	21.50	1.10×10^{-1}	This study
	0.0120	0.0014	58.0	21.50	2.24×10^{0}	This study
	0.0060	0.001	116.0	21.50	1.116×10^{1}	This study

Note: Tissue half-life is calculated as $\ln(2)/\lambda$. Values from this table were used to draft Fig. 3.

*Whole organism sampled as opposed to white muscle tissue.

†Values taken from Herzka 2005.

differences observed in the natural abundance of carbon isotopes between energy sources are of limited use in understanding short-term feeding changes in larger or older life stages. MacAvoy et al. (2001) concluded that long half-lives of carbon in muscle tissue precluded detecting an isotopic signal in adult blue catfish (*Icatlurus furcatus*) feeding on migratory prey fishes with a distinctly different isotopic value. Estimates of tissue half-lives are required to determine the duration of feeding or the difference in $\delta^{13}C$ of the diet necessary to detect a change in the $\delta^{13}C$ of these larger consumers. Conversely, short half-lives of carbon indicate tissue $\delta^{13}C$ measurements may only represent recent dietary $\delta^{13}C$ and do not necessarily integrate dietary information over longer time periods. Fish tissues with short half-lives would be useful for inferring short-term changes in behavior or migration, whereas long half-life tissues would be useful for inferring longer-term phenomena such as average annual food web connections.

Table 6. Model results and parameter values for models relating the natural log of the rate of isotopic change (λ) to the natural log of fish mass (M), and water temperature (T, in Kelvin).

Model	N	r^2	AIC	$a \pm$ SE	$b \pm$ SE	$c \pm$ SE
$\log(\lambda) = a + b\log(M)$	36	0.71	78.8	–3.65±0.17*	–0.20±0.02*	
$\log(\lambda) = a + b\log(M) + c_1(T^{-1})$	36	0.72	80.8	–2.46±7.89	–0.20±0.02*	346.99±2319.04
$\log(\lambda) = a + b\log(M) + c_2(T)$	36	0.72	80.7	–15.51±9.65	–0.22±0.03*	0.04±0.03

Note: In the second equation, $c_1 = -E_a/k$. Regression coefficients noted with an asterisk (*) were significant at $p < 0.001$.

Factors affecting carbon turnover rates

In reviewing the state of biological isotope ecology, Martínez del Rio et al. (2009) note ecologists should understand isotopic turnover rates and factors that influence those rates to (*i*) determine the time window through which tissues reflect dietary isotope change and (*ii*) explore resource use variability through tissues with different turnover rates. We would add that understanding relationships between turnover rates and simple gradients, such as body size, increase the utility of stable isotopes to quantify material transport in food webs rather than simply providing qualitative descriptions (Schindler and Lubetkin 2004). Combining rates of carbon isotope change from this and other studies, we established a significant negative relationship between fish size and the rate of isotopic change. McIntyre and Flecker (2006) found similar evidence for the negative scaling of nitrogen isotope change with body size in tropical ectotherms. While the slope of the fish size and carbon turnover rate relationship was similar to –0.25, which has been proposed for some allometric-based metabolic models, it is important to recognize this particular exponent is not universally accepted (Glazier 2010). The intention of our comparison was not to support or reject specific metabolic scaling coefficients, but rather to draw attention to the utility of metabolic theory in understanding isotopic incorporation rates in animals. The proposed allometric relationship relating dorsal muscle λ and fish mass can be used to approximate the value of muscle λ and half-life based solely on fish mass and thereby aid ecologist's interpretation of isotopic patterns.

We expected that including temperature as a predictive variable along with mass would improve our capability to estimate λ (Gillooly et al. 2001). Including the temperature term in the regression model slightly increased the predictive capacity from $r^2 = 0.61$ (mass alone), to $r^2 = 0.62$ (mass and temperature) and, based on AIC, the improvements were not adequate to support the additional parameter in the model. The ranges of temperature and fish size examined likely limited the improvement in the two parameter model. In those studies that reported both a measure of water temperature and fish size, the range of temperatures considered (14–24 °C) would approximately double metabolic rate, whereas the mass range (0.00012–434 g) would cause a sixfold change in metabolic rate (Clark and Johnston 1999). The positive coefficient of temperature in models predicting λ supports the positive influence of temperature on the rate of isotopic change (Bosley et al. 2002; McIntyre and Flecker 2006).

The utility of carbon stable isotopes in defining energy sources and visualizing niche space has been well established (France 1995; Vander Zanden and Vadeboncoeur 2002). To move beyond static linkages and employ carbon stable isotopes to quantify nutrient or energy flux in food webs, we must have an estimate of the dietary legacy that a consumer's $\delta^{13}C$ represents. By taking advantage of a ^{13}C addition in a natural system, we demonstrated this legacy can range from a week to multiple years within a single lake fish community. We found carbon stable isotope change in muscle tissue is not solely regulated by growth, but that metabolic replacement influences the rate at which a consumer's muscle $\delta^{13}C$ comes to reflect the $\delta^{13}C$ of their diet. In short, fish size has a fundamentally important role in the rates of stable isotope changes for fish muscle tissue. By combining bioenergetic models with frequent dietary $\delta^{13}C$ estimates, we established a method to determine isotopic turnover and its components in natural systems where consumers exhibit dramatic changes in dietary $\delta^{13}C$.

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Detecting and forecasting complex nonlinear dynamics in spatially structured catch-per-unit-effort time series for North Pacific albacore (*Thunnus alalunga*)

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Abstract: The presence of complex, nonlinear dynamics in fish populations, and uncertainty in the structure (functional form) of those dynamics, pose challenges to the accuracy of forecasts produced by traditional stock assessment models. We describe two nonlinear forecasting models that test for the hallmarks of complex behavior, avoid problems of structural uncertainty, and produce good forecasts of catch-per-unit-effort (CPUE) time series in both standardized and nominal (unprocessed) form. We analyze a spatially extensive, 40-year-long data set of annual CPUE time series of North Pacific albacore (*Thunnus alalunga*) from $1^\circ \times 1^\circ$ cells from the eastern North Pacific Ocean. The use of spatially structured data in compositing techniques improves out-of-sample forecasts of CPUE and overcomes difficulties commonly encountered when using short, incomplete time series. These CPUE series display low-dimensional, nonlinear structure and significant predictability. Such characteristics have important implications for industry efficiency in terms of future planning and can inform formal stock assessments used for the management of fisheries.

Résumé : La présence d'une dynamique complexe et non linéaire dans les populations de poissons et l'incertitude concernant la structure (forme fonctionnelle) de cette dynamique posent des défis en ce qui à trait à l'exactitude des prédictions faites par les modèles traditionnels d'évaluation des stocks. Nous décrivons deux modèles non linéaires de prédiction qui recherchent les signes d'un comportement complexe, évitent les problèmes de l'incertitude structurale et produisent de bonnes prédictions de séries chronologiques de captures par unité d'effort (CPUE) à la fois de forme standardisée et de forme nominale (non traitée). Nous analysons une banque de données à large représentation spatiale couvrant 40 années de séries chronologiques annuelles de CPUE de germons (*Thunnus alalunga*) du Pacifique Nord provenant de cellules de $1^\circ \times 1^\circ$ de l'est du Pacifique Nord. L'utilisation de données à structure spatiale dans les techniques de composition améliore les prédictions de CPUE au-delà des échantillons et surmonte les difficultés couramment rencontrées à l'utilisation de séries chronologiques courtes et incomplètes. Ces séries de CPUE possèdent une structure à faible dimension et non linéaire et une prédictibilité significative. De telles caractéristiques sont de grande importance pour la planification efficace future par l'industrie et peuvent enrichir les évaluations formelles de stocks utilisées dans la gestion des pêches.

[Traduit par la Rédaction]

Introduction

Marine populations typically vary across a broad spectrum of space and time scales. Understanding the causes of population fluctuations and their implications for management remains a primary objective of fisheries research (Sissenwine 1984; Sissenwine et al. 1988). Observed patterns of variability in marine populations have been classified along a continuum from steady state to "irregular" and "spasmodic" dynamics (Caddy and Gulland 1983; Spencer and Collie 1997). It has long been recognized that both nonlinear population processes and environmental forcing can generate dra-

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matic fluctuations in recruitment of marine fish and invertebrate stocks. Ricker (1954) provided the first demonstration of the potential for what is now called chaotic population dynamics in highly nonlinear systems, memorably describing the transition to chaos as involving "increasingly violent oscillations" in recruitment.

Nonlinear population dynamics can result from a variety of sources, including (*i*) multiplicative interactions between species or with physical variables (Dixon et al. 1999); (*ii*) high intrinsic growth rates with regulatory time lags (May 1976; Anderson et al. 2008); (*iii*) stochastic process noise or nonlinear amplification of stochastic physical forcing (Dixon et al. 1999; Sugihara 1994); (*iv*) low-frequency environmental variability driving a system across multiple stable states (Steele and Henderson 1984); (*v*) the tendency for large pelagic fishes to track low-frequency variability while "smoothing" high-frequency variability (Steele and Henderson 1984); or (*vi*) density-dependent dynamics, such as mortality and growth at early life history stages, interacting on multiple time and space scales (Royer and Fromentin 2006). Bakun (2001) outlined several fisheries-related observations consistent with the presence of nonlinear dynamics, such as the ephemeral nature of correlations with environmental variables and the failure of some collapsed populations to regain prior levels of productivity after fishery closures.

Nonlinear ecological interactions among components of the system and external perturbations due to natural and anthropogenic forcing factors have the potential to result collectively in extremely complex dynamics. Human interventions related to fishing intensity in response to economic forces (Berryman 1991; Conklin and Kolberg 1994), management strategies directed at size- and species-selective harvesting (Basson and Fogarty 1997), and remedial action such as artificial enhancement (Fagen and Smoker 1989) all have been shown to affect the probability of observing complex dynamics, including chaos, in these systems. The hallmark of a complex adaptive system is variability and surprise (Scheffer et al. 2009) — the potential for multiple stable states and rapid transitions in system dynamics requires that adaptive management structures be put in place to cope with unanticipated change.

The recognition that time series of population estimates potentially contain the signature of complex dynamical behaviors that can be separated from measurement error and stochastic forcing has revolutionized our ability to dissect the underlying causes of fluctuations in populations (Sugihara and May 1990; Tsonis and Elsner 1992; Sugihara 1994). These methods have now been applied to a number of marine systems (Dixon et al. 1999; Hsieh et al. 2005; Anderson et al. 2008). The nonlinear time series analysis underlying this approach employs a flexible nonparametric model structure and does not depend on an a priori specification of the governing equations for the system. This holds great advantage in marine fishery systems where model or structural uncertainty is often difficult to identify and quantify (Fogarty et al. 1997). Structural uncertainty in critical population and ecological processes (and in how they may change over time) can substantially degrade our ability to develop forecasts of population and ecosystem states (Charles 1998; Breiman 2001).

Relevant indicators of change in complex fisheries systems include commonly observed metrics such as catch per unit effort (CPUE), used both directly as an index of abundance or indirectly as an auxiliary variable in population models (Maunder and Punt 2004). In this paper, we investigate the dynamics of juvenile North Pacific albacore (*Thunnus alalunga*) using CPUE time series from the eastern North Pacific Ocean commercial troll fishery. We explore the use of spatially disaggregated data to increase information density based on the time series composite method of Sugihara (Sugihara 1994; Sugihara et al. 1996; Hsieh et al. 2008). Our objective is to test for hallmarks of nonlinear dynamics in these series and to produce annual forecasts of CPUE at two scales: (*i*) the entire region covered by the data and (*ii*) individual spatial cells (described below). This general approach can serve as an important complement to other fishery modeling and assessment methods.

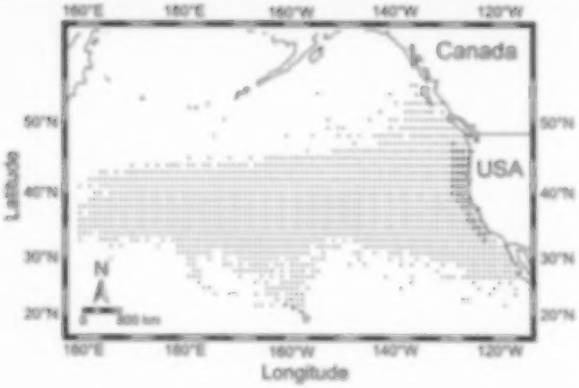
Materials and methods

Data

North Pacific albacore are a single stock of highly migratory tuna confined to the North Pacific basin. The juvenile and adult subpopulations tend to occupy distinct regions of the Pacific and are harvested by separate fisheries (Otsu and Uchida 1963; Childers and Betcher 2008). Spawning occurs in the central western North Pacific Ocean (Laurs and Lynn 1977), and juveniles migrate into the productive California Current System (CCS) or the Kuroshio Current System (Kimura et al. 1997). Juveniles reside in the CCS from late spring to late fall, where they are harvested by the US, Canadian, and Mexican surface fleets. This albacore population does not have a history of rapid depletions, but catch rates are highly variable on an annual scale (ISC (International Scientific Committee for Tuna and Tuna-Like Species in the North Pacific Ocean) 2007). Decadal-scale differences in population estimates generated hypotheses during the 2004 stock assessment (Stocker 2005) that the population may contain periods of low (1975–1989) and high (1990–2000) productivity; however, these trends were less pronounced in the following stock assessment (ISC 2007) and require further study.

We analyze catch (number of fish) and effort (boat-days) from the US commercial troll fishery for North Pacific albacore in monthly $1^{\circ} \times 1^{\circ}$ spatial coordinates (hereafter, cells) from 1966–2005. The fishery lands juvenile albacore (ages 1–4) and is geographically centered in the CCS, although effort can extend into the central North Pacific gyre (Fig. 1). Data were obtained from voluntary submissions of logbooks, with approximately 20% vessel coverage (ISC 2007). Annual CPUE (x_t) for each spatial cell (Walters 2003) was calculated by summing catch and effort from June to October, the primary fishing season when albacore are present in the CCS. Few cells contained complete time series. Of 1366 cells containing a possible 40 years of data, 138 cells contained at least 20 years of data, 39 cells contained at least 35 years, and only 7 cells contained all 40 years of data (Figs. 1 and 2). Analysis was performed on normalized (mean = 0, standard deviation (SD) = 1) first differences ($\Delta x = x_{t-1} - x_t$). Such transformation removes secular trends

Fig. 1. Spatial cells (1° × 1°) containing catch and effort data from the US commercial troll fishery for juvenile albacore, 1966–2005. Small markers, ≥1 year of data; large markers, ≥35 years of data.



in data and allows compositing of series that may have different magnitudes and variances (described below).

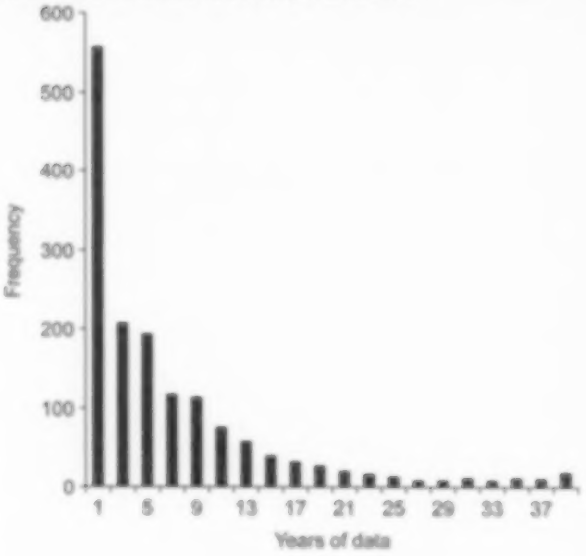
Nonlinear forecasting

We define nonlinear dynamics as those for which the deterministic component $\phi(X)$ and the stochastic component $\phi(\varepsilon)$ are not additive, i.e., $\phi(X + \varepsilon) \neq \phi(X) + \phi(\varepsilon)$, and the resulting dynamics are unstable (exhibiting sensitive dependence on initial conditions). Nonlinear forecasting models are nonparametric statistical models that do not make assumptions about the underlying functional form of the system. Rather, they utilize the structure of the observed data itself to make forecasts. Consequently, one of their strengths is the ability to extract information about dynamical complex systems despite ignorance of the true dynamics. Another strength is that these models are parsimonious in their lack of free (fitted) parameters. For most applications, the basic model contains only one free parameter (dimensionality, as explained below).

Research has established these methods in a host of fields (Farmer and Sidorowich 1987; Casdagli 1992), including epidemiology (Sugihara and May 1990), cardiology (Sugihara et al. 1996), atmospheric science (Sugihara et al. 1999), ecology (Hsieh et al. 2005), behavior (Maye et al. 2007), and astronomy (Kilcik et al. 2009). However, they rarely have been used in fisheries science, despite the inherent complexity of and uncertainty about the systems under study. The two forecasting models described here, simplex projection and sequential locally weighted global linear maps (or S-maps), have complementary purposes; simplex projection calculates the dimensionality or degrees of freedom of the data (defined in the following paragraph), and S-maps classify the data as linear or nonlinear. Both models produce forecasts, and because they pose different questions about the data, the answers to which are ecologically important and relevant for modeling, we use them in concert.

The dynamics of a population are constrained by the action of N variables, or dimensions. In nature, these may be hundreds of physical and biological variables in the species' environment. A time series is merely a one-dimensional observation of the effects of those variables on the population.

Fig. 2. Number of years with catch-per-unit-effort data in each of the 1366 spatial cells of juvenile North Pacific albacore harvested by the US commercial troll fishery, 1966–2005.



Fortunately, in dissipative (thermodynamically open) systems such as ecosystems, high-dimensional dynamics often collapse to simpler, low-dimensional dynamics, and a major part of the variability in the system can be modeled with relatively few variables (Schaffer and Kot 1985; O'Neill 1986; Crutchfield and McNamara 1987). The subset of these variables defines a state space in which each axis of the space corresponds to one variable, and in a dynamic system, the set of trajectories that define the movement of the observations in that space is called an attractor (Fig. 3). Over a sufficient time horizon, the path the observed variable traces within the state space defines the attractor, and perturbations to the system eventually return to that attractor. The geometry of these low-dimensional attractors can then be used to forecast the trajectory of an observed component variable, such as a targeted fish stock, by simply following the path of the attractor through time (Lorenz 1963).

We begin by identifying a small, thus tractable, set of dimensions for modeling that will result in the best predictability for the data. Typically, the key dimensions will be unknown variables; however, a mathematically similar version of the real attractor (a shadow attractor) can be constructed from time lags of the series, such that the lags represent the unknown variables. This is a direct implication of Takens' Theorem (Takens 1981), which demonstrates the lags of a time series can be used as proxies for the unknown dimensions shaping an attractor. These lags become axis coordinates, creating a univariate embedding that captures the characteristics of the real attractor (Takens 1981; Sugihara and May 1990). An embedding is simply the shadow attractor that results from plotting the time series against lags of itself, where each time-lagged axis is one dimension. A conceptual example of a time-lagged embedding is shown using observations of annual CPUE for juvenile North Pacific al-

Fig. 3. Time-lagged embedding for annual catch-per-unit-effort data from 43°N, 127°W, 1966–2005. (*a*) The time series shows changes in annual catch rate. (*b*) A two-dimensional plot of x_t versus x_{t-1} hints at underlying structure in the data. (*c*) A three-dimensional lagged-coordinate plot displays more coherent geometry, suggesting the presence of an attractor in the data.

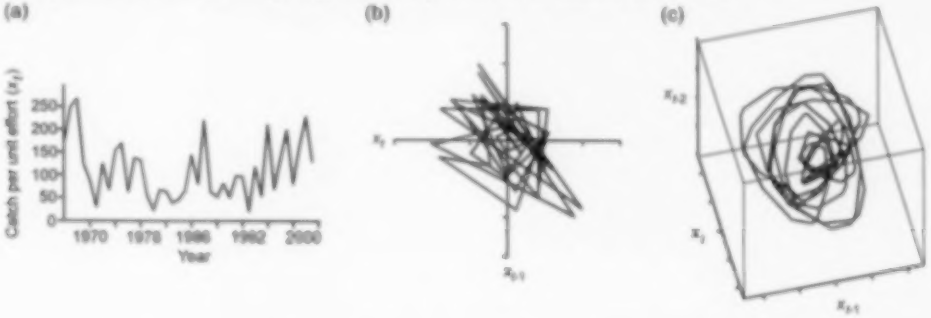
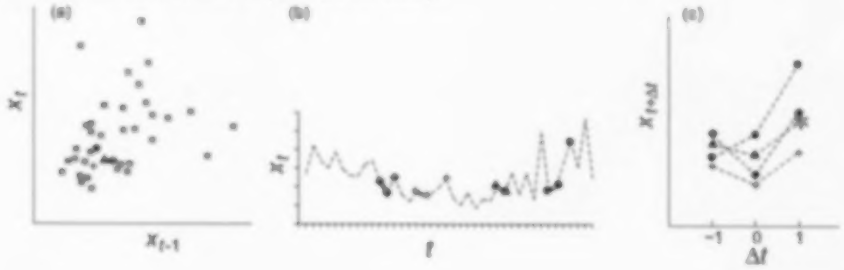


Fig. 4. Simplex projection (illustrated for $E = 2$, where E is the embedding dimension). We analyzed the data in increasingly higher dimensions (in this study, E ranged from 1 to 10), and the dimensionality that resulted in the highest forecast skill (ρ) or lowest mean absolute error (MAE) was chosen. (*a*) An embedding was created by plotting time lags of the data (for two dimensions, x_t versus x_{t-1}). The non-triangles are the set of library vectors from which the model was built. The triangle is the prediction vector that produced the forecast. The Euclidean distances between the prediction vector and all library vectors were calculated, and the $E+1$ nearest neighbors (black non-triangles) were selected. (*b*) The nearest neighbor library vectors (non-triangles) and prediction vector (triangles) are shown in relation to the one-dimensional time series. The one-step-ahead trajectory of the library vectors, x_{t+1} (non-triangles, connected by dashed line to library vector), determines the value of the forecast. (*c*) The forecast (*) is an exponentially weighted average of the $E+1$ nearest neighbor library trajectories, where trajectories are inversely weighted according to the distance of the nearest neighbor to the prediction in the embedding. Note the axes in panel (*c*) have been rescaled relative to panel (*b*) for clarity.



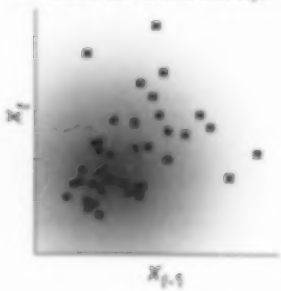
bacore (Fig. 3). The familiar one-dimensional time series (time, x_t) shows changes in annual catch rate. A two-dimensional embedding (x_{t-1}, x_t) begins to display a repeating pattern. In three dimensions (x_{t-2}, x_{t-1}, x_t), the geometry of the attractor becomes even more coherent.

In this study, nonlinear forecasting using CPUE time series was used to (*i*) calculate the number of dimensions needed to describe the time series; (*ii*) classify the time series as linear or nonlinear; and (*iii*) make 1-year-ahead forecasts. First, the simplex projection model (Sugihara and May 1990) identified the best embedding dimension (E) for the data. Second, this E-dimensional embedding was used in the S-maps model (Sugihara 1994) to assess the nonlinearity of the time series. Forecasts were produced using both models. The criteria for model performance is forecast skill (ρ, Pearson's correlation coefficient), measured as the correlation between observed and forecasted values, and mean absolute error (MAE), the absolute value of the difference between observed and predicted values. The nonlinear forecasting models are outlined briefly below. A more rigorous mathematical treatment of these methods can be found in Sugihara and May (1990) and Sugihara (1994).

Simplex projection

The simplex projection model is a nearest neighbor algorithm that uses the shape of the shadow attractor to follow the trajectory of the data when embedded in E-dimensions. We analyzed successively higher-dimensional embeddings (*t*s in Fig. 3). For this study, we varied E from 1 to 10. The embedding creates vectors formed from the data of length E. One set of vectors is used to build the model, dubbed the library set, and a second set of vectors is used to test the ability of the model to make forecasts, dubbed the prediction set (see Fig. 4*a* for an example where $E = 2$). For any given prediction vector (Fig. 4*a*, triangle), the $E+1$ nearest neighbors are chosen from the library vectors (Fig. 4*a*, squares) based on the shortest Euclidean distances. The $E+1$ nearest neighbors are called the simplex (the minimum number of points required to surround a prediction vector in an E-dimensional space). The forward projection of the nearest neighbor vectors to time $t+1$ dictates the trajectory of the prediction vector to time $t+1$, generating the forecast (Fig. 4*c*, asterisk). The forecast is a weighted average of the nearest neighbor values at time $t+1$ with weights depending exponentially on the distance of the neighbors

Fig. 5. S-maps (illustrated for $E = 2$). As in simplex projection, an embedding is created by plotting time lags of the data (for two dimensions, x_t versus x_{t-1}). A global linear model is compared with locally weighted nonlinear models. The location of the prediction vector (triangle) is calculated based on the location of the library vectors (squares). In the linear model, equal weighting is applied to all library vectors in the embedding. In the nonlinear models, the library vectors are weighted exponentially according to their Euclidean distance from the prediction vector, with closer vectors receiving a higher weighting (background shading). The model becomes increasing more nonlinear according to the tuning parameter θ. The linear model is given by $\theta = 0$, and the nonlinear models are $\theta > 0$, so models are nested and equivalent.



to the prediction vector at time t. That is, the weighting is determined at time t and applied to time $t+1$ for the forecast.

If the time series is long enough, the sets of library and prediction vectors are mutually exclusive (e.g., the first and second halves of the data). For short time series, we use cross-validation, for which only the prediction vector is held out of sample. The model accommodates missing values by excluding from the library or prediction sets any vector that would include a missing point. Forecasts for the prediction set are made at each time step, beginning with $x_{t=(E-1)}$ (to accommodate the length of the first vector). Forecast skill (ρ) and MAE are then calculated from the observed and forecasted values. As the geometry of the attractor changes with higher-dimensional embeddings (see Fig. 3), the library vectors defined as "nearest" may change. Thus, each successive embedding will produce different forecasts, and the E that results in the highest ρ and (or) lowest MAE is identified as the "best" embedding dimension for the data. In the majority of cases, the lowest MAE corresponds with the highest ρ. In cases in which there is a discrepancy, the metric that corresponds to the highest number of predictions (lowest E) is chosen. In our experience (unpublished data), cases in which there is a discrepancy in the best E identified by MAE and ρ occur for extremely noisy data, and the model ρ is rarely statistically significant (i.e., the model is not able to forecast the data). In simplex projection, E is the only free model parameter.

S-maps

S-maps classify a time series as linear or nonlinear based on the level of forecast skill obtained from equivalent linear or nonlinear models. The data are embedded based on the best E obtained using simplex projection. Again, the data are divided into sets of library vectors and prediction vectors (Fig. 5). The forecast is the location of the prediction vector at time $t+1$, calculated based on the locations of all the library vectors (in comparison with simplex projection, which uses only $E+1$ library vectors). In the global linear model, equal weighting is applied to all library vectors in the embedding. In the nonlinear models, the library vectors are weighted exponentially according to their Euclidean distance from the prediction vector, with closer vectors receiving a higher weighting when computing coefficients. A series of nonlinear models, with progressively greater weighting given to the localized neighborhood in the reconstructed state space, are analyzed.

S-maps produce forecasts governed by a nonlinear tuning parameter, θ. Specifically, for any given time step t, the set of library vectors is $\{\boldsymbol{x}_i\}$ (Fig. 5, squares) and the prediction vector is $\boldsymbol{x}_t$ (Fig. 5, triangle). The set of time series values at time $i + 1$ for library vectors is $\{y_i\}$, and the unknown forecast for $\boldsymbol{x}_t$ is $\hat{y}_t$. Setting $\boldsymbol{x}_t(0) = 1$, then

$$\hat{y}_t = \sum_{j=0}^{E} c_t(j)x_t(j)$$

and $\boldsymbol{c}$ is solved by singular value decomposition (with a singularity threshold of 10^5) as

$$\boldsymbol{b} = \mathbf{A}\boldsymbol{c}$$

where $\boldsymbol{b}(i) = w(\|\boldsymbol{x}_i - \boldsymbol{x}_t\|)y_i$ and $\mathbf{A}(i, j) = w(\|\boldsymbol{x}_i - \boldsymbol{x}_t\|)x_i(j)$ and

$$w(d) = e^{-\theta d/\bar{d}}$$

where $w(d)$ is the weighting function, d is the Euclidean distance between a given library vector ($\boldsymbol{x}_i$) and the prediction vector ($\boldsymbol{x}_t$), and $\bar{d}$ is the mean Euclidean distance between all neighboring vectors (Sugihara 1994). For the matrix $\mathbf{A}$, j corresponds to the E time lags in each library vector such that each library and prediction vector has length E.

The model becomes increasingly nonlinear according to the tuning parameter θ. Note that the linear model is simply $\theta = 0$ and the nonlinear models are $\theta > 0$, so the models are nested and equivalent. For the linear model, an S-map is essentially an autoregressive model of order E, for which the same coefficients apply to each prediction vector. For $\theta > 0$, new coefficients are calculated for each prediction vector with weights depending on where the vector is in the reconstructed state space. As θ increases, the forecasts rely more strongly on the values in the local neighborhood (represented by the darker shading in Fig. 5). The data are nonlinear if greater weighting of the local neighborhood of library vectors results in a better model than that achieved from equally weighting all data (Casdagli 1992; Sugihara 1994). In S-maps, both E and θ are free parameters.

As with simplex projection, the best model produces the highest out-of-sample forecast skill (ρ) and (or) lowest error (MAE). The degree of nonlinearity is measured as $\Delta\rho_\theta = \rho_{\theta>0} - \rho_{\theta=0}$ and $\Delta\text{MAE}_\theta = |\text{MAE}_{\theta>0} - \text{MAE}_{\theta=0}|$. The significance of $\Delta\rho_\theta$ is measured with Fisher's Z test; with time series that contain significant serial autocorrelation (as with these CPUE data), $\Delta\rho_\theta$ can be a biased measure of nonlinearity (Hsieh and Ohman 2006). We therefore test the significance of the improvement in error, ΔMAE_θ, with a randomization procedure outlined in Hsieh and Ohman (2006). ΔMAE_θ for the model is calculated and treated as a

test statistic. Then, the order of the time series is shuffled, S-maps are used to model the shuffled time series, and a new ΔMAE_θ is calculated. This procedure is repeated 500 times to create a null distribution for ΔMAE_θ, against which the significance of the test statistic is measured. A series was classified as nonlinear if the significance of ΔMAE_θ exceeded $\alpha = 0.1$.

Formation of composite attractors

The dimensionality and forecast skill achieved with these methods is not absolute but is related to the amount and quality of the data available (i.e., the length of the time series and the amount of observational error). Short time series, often characteristic of CPUE data, may have low predictive skill and make identification of the dynamics (e.g., linear versus nonlinear, high-dimensional versus low-dimensional) difficult. This difficulty may be overcome by combining spatially structured CPUE series in a way that exploits the amount of data available. Specifically, time series from many spatial cells are combined into one composite library set, so that the embeddings are generated from all individual time series, resulting in a denser attractor. This has the net effect of increasing the length of time over which we have observed the dynamics, allowing us to see the system in more (and different) states than with a single time series.

We investigate the effect of using composite libraries to produce nonlinear forecasts for these CPUE data. Regarding these models, there is no rule defining the length of a time series required for sufficient information; forecast skill is a function of the levels of observation noise, the underlying complexity (E), and the degree of nonlinearity in the data. Forty years of data (available here) may produce good forecasts if the system is low-dimensional and the data contain a strong signal. However, if 40 years are insufficient, compositing can greatly enhance the underlying signal in the data without altering the dynamics contained in the individual series (Hsieh et al. 2008). By contrast, simple averaging or other linear transformations of data have been shown to obscure dynamics (Sugihara et al. 1990, 1999).

This compositing approach, used to analyze human heart rhythms (Sugihara et al. 1996), validated with model data, and applied to a multispecies ichthyoplankton data set (Hsieh et al. 2008), is appropriate if a key assumption is met: that all time series included in the composite are generated by the same dynamic process at some level of resolution (scale). It is likely the case of this albacore subpopulation (same fishery, region, and age group) that different time series are realizations of the same underlying processes that govern CPUE dynamics. Because albacore are highly migratory and the same subpopulation moves in and out of cells, time series from any given cell contains CPUE information that was likely to be generated by the same dynamics that govern the entire subpopulation. Even if albacore abundance or environmental conditions (e.g., temperature, forage) vary between cells, the underlying dynamic process may still be the same, in which case the time series need only to be scaled (normalized). We pose a specific test for this hypothesis: if the forecast skill of the model is improved when a composite library is used, then the dynamic process is homogeneous. If the dynamics are different, the inclusion of time series from heterogeneous processes would not improve forecast skill (and, in fact, might decrease it).

One goal of this study is to produce forecasts of CPUE at two spatial scales: the entire region and individual cells. The former was accomplished by creating a composite from all 1366 time series, providing a baseline for how well the model can simultaneously forecast the full data set. The latter was accomplished by comparing two approaches: (*i*) using the data from a single cell to forecast itself (where $n \leq 40$ years and using cross-validation) or (*ii*) using a composite library built from other cells to forecast (out-of-sample) the time series in a single target cell. The first approach is limited by the amount of data in any given cell, whereas the second approach will not produce good forecasts if other cells confound the signal (i.e., dynamics are heterogeneous).

We therefore examined three configurations of the time series. First, a composite built from all 1366 cells that contained data was analyzed as a whole; this is referred to as the full-composite. The full-composite describes the dynamics of the subpopulation at the scale of the sampling region and provides a baseline for comparing results from single cells (and for comparing analyses of the standardized time series, described below). Second, single cells were analyzed by forecasting themselves (dubbed single cell analysis). For each cell, E and θ were determined independently. Given the constraints imposed by short and incomplete time series, we selected the 39 cells that contained at least 35 years of data for this analysis. Third, a composite library set was constructed from 1365 cells, forecasting one excluded target cell; this is referred to as the target-composite. The target cells were the same 39 data-rich cells used in the single cell analysis. This third configuration tested whether a composite library improved the model forecast skill in comparison with a library generated from data in the single cell only.

In all analyses, forecasting was performed out-of-sample. In both the full- and target-composites, all occurrences (from other cells) of the year in the prediction vector were excluded from the library. That is, if the model was predicting the year 1977 in the target cell, all occurrences of 1977 were excluded from the composite library. The full-composite was long enough also to be divided into a library half and a prediction half (each containing 683 time series). Because results may vary depending on which series are in the library or prediction halves of the composite, we randomly shuffled the time series between library and prediction halves (500 times) and computed average statistics for the full-composite. In the case of the target-composites, the library (1365 cells) and prediction (1 cell) sets were mutually exclusive. Finally, when analyzing single cells, cross-validation was used so that the prediction vector was excluded from the library set.

Standardized CPUE

Estimates of albacore population size generally rely on fishery-dependent CPUE observations (Stocker 2005; ISC 2007), a measurement that can provide a relative index of abundance if certain assumptions are met. The primary assumption is that local catchability, or the fraction of fish in the environment caught by one unit of effort, remains constant as data are analyzed at different time and space scales.

This assumption is frequently violated (Harley et al. 2001), and methods for standardizing CPUE time series are designed to remove the confounding effects of variables exogenous to abundance that could systematically affect observations of CPUE (Maunder and Punt 2004). Standardization methods model CPUE as a function of independent variables; these typically include obvious influential factors such as time (e.g., year, month, season) and spatial location (e.g., latitude, longitude, distance from shore), but they can also include variables such as sea surface temperature, gear type, fishing nation, vessel information, etc. The statistical year effect produced from the model is the standardized CPUE, a single time series that represents assimilated data for an entire spatial domain. Thus, in addition to analysis of the nominal data described above (annual catch divided by annual effort in a cell), in this study we also consider a standardized CPUE series because they are frequently used in stock assessment models and as such may have immediate utility.

We implement a generalized linear model (GLM), the most common standardization method in use, to produce one standardized time series for the full data set. The model and data treatment were chosen based on the method used in albacore stock assessment (ISC 2007), described in McDaniel et al. (2006). Data were filtered to remove points with fewer than 3 days of total effort in a given cell-month. The model was $\log_e(\text{CPUE}_{ijk} + 1) = \text{year}_i + \text{season}_j + \text{area}_k + \varepsilon_{ijk}$, where "year" is 1966–2005; "season" is spring (April–May–June), summer (July–August–September), or fall (October–November–December); "area" is offshore (west of 130°W longitude) or inshore; and $\varepsilon \sim N(0, \sigma^2)$. The coefficients estimated for the year effect were back-transformed from logarithms for nonlinear forecasting.

The GLM was investigated in two ways, analogous to the approach used with (nominal) single cells. First, we analyzed the GLM as a single series (i.e., the series predicting itself using cross-validation; dubbed GLM-single) to investigate whether the dynamic complexity of the nominal CPUE data was preserved through the data assimilation that occurs with standardization. Second, the full-composite of 1366 nominal series was used as a library to predict the standardized CPUE (dubbed GLM-composite). This was done to see if the data-rich attractor reconstructed from the compositing of these extensive spatially resolved data could be used to improve forecasts of the standardized CPUE.

Results

The statistics for all configurations of the data are summarized (Table 1). Time series of nominal CPUE for juvenile North Pacific albacore exhibit low-dimensional, weakly nonlinear structure. The full-composite identified $E = 5$ (rounded from a mean of 4.7 over all 500 shufflings) as the best embedding dimension using simplex projection and classified the time series as nonlinear using S-maps. After excluding from the model vectors that would contain a missing data point, over 1000 forecasts were produced.

In general, use of the target-composite library to forecast individual cells produced better forecasts than the single cell analysis (Fig. 6). For the 39 target cells, the composite library outperformed (based on higher forecast skill, ρ) the use of the single cell to forecast itself in 35 of 39 cells using simplex projection and in 27 of 39 cells using S-maps. Using simplex projection, the target-composite identified, on average, an E of 5, whereas the single cells predicting themselves identified a mean E of 3. The composite library also increased the likelihood of detecting a nonlinear signal in the data. Ten of 39 time series (including all seven complete time series) were identified as nonlinear when a single cell was used to forecast itself. However, using the composite library, the model identified 17 of 39 as nonlinear.

The GLM-standardized series also contained a nonlinear signature, but only when the composite library was used. The forecast model with the highest skill was produced from simplex projection using the standardized series to predict itself (GLM-single; Table 1). That is, for simplex projection, the use of the full-composite library (made of 1366 nominal time series) did not improve forecast skill. The GLM-single analysis identified $E = 2$, whereas the GLM-composite identified $E = 5$. We demonstrate how 1-year-ahead forecasts are produced with this method (Fig. 7). Because forecast skill was highest with simplex projection ($\rho = 0.8$), this model was used to generate a forecast for 2006 using the standardized time series from 1966 to 2005. Interestingly, the root mean squared error of the GLM model (McDaniel et al. 2006) was significantly higher than the root mean squared error associated with forecasting the GLM using simplex projection (0.61).

Discussion

The ability to model albacore in few dimensions suggests the dynamics of CPUE are primarily driven by a small number of key variables. Furthermore, these dynamics are (weakly) nonlinear and predictable, allowing future catch rates to be modeled. From Takens' Theorem (Takens 1981), the E needed to reconstruct the state space can be bounded by $D < E < 2D + 1$, where D is the dimensionality of the (true, unobserved) system attractor. An E of 5 (calculated for the full composite) therefore translates to system dimensionality of between 2 and 4 (Casdagli 1992; Sugihara 1994). Consequently, it should be possible to identify which oceanographic or biological variables influence catch rate (Dixon et al. 1999). Factors that may determine albacore local abundance or catchability (but have not been shown to regulate population abundance) include sea surface temperature, chlorophyll *a* concentration, and forage availability (Laurs and Lynn 1977; Polovina et al. 2001; Zainuddin et al. 2006).

The nonlinear signal detected in these data is weak but present at certain scales and if sufficient data are available. We find conclusive evidence of nonlinearity (statistically significant decreases in MAE) in the full-composite, 44% of the target-composites, 25% of the single cells, and in the GLM-composite. The ability to detect any nonlinearity at all is remarkable given the constraints of spatial scale (Sugihara et al. 1999), time series length (Hsieh et al. 2008), and the presence of observation noise (Sugihara 1994). For the seven complete time series available (40 years long), all were nonlinear. The degree of nonlinearity ($\Delta\rho$) was related to the length of the target time series being forecast (R^2 =

Table 1. Summary statistics for nonlinear forecasting models predicting albacore catch per unit effort (CPUE).

		Simplex projection				S-maps				
Data configuration	No. of forecasts	E	ρ	ρ p value	MAE	θ	ρ p value	MAE	ΔMAE	ΔMAE p value
Full-composite	1089±147[a]	4.7±0.61[a]	0.46±0.01[a]	<0.0001[a]	0.64±0.01[a]	0.56±0.01[a]	<0.0001[a]	0.58±0.01[a]	0.02±0.003[a]	<0.01[a]
Target-composite	27±5.5[b]	4.9±2.4[b]	0.58±0.1[b]	39 of 39*	0.56±0.10	0.59± .1[b]	39 of 39*	0.59±0.07[b]	0.04±0.04[b]	17 of 39**
Single cells	27±5.5[b]	2.8±2.0[b]	0.35±0.2[b]	24 of 39*	0.61±0.12	0.52±0.2[b]	36 of 39*	0.63±0.10[b]	0.02±0.03[b]	10 of 39**
GLM-single	38	2	0.80	<0.0001	0.50	0.63	<0.0001	0.62	0.0007	NS
GLM-composite	34	5	0.64	<0.0001	0.58	0.68	<0.0001	0.56	0.06	0.04

Notes: E is embedding dimension, ρ is model forecast skill, mean absolute error (MAE) is model error, ΔMAE measures the improvement of the nonlinear over the linear model; GLM is generalized linear model. *, number of series with forecast skill significant at $\alpha = 0.05$; **, number of series with significant nonlinearity at $\alpha = 0.10$.

[a]Mean ± standard deviation (SD) of 500 randomizations.

[b]Mean ± SD of 39 series.

0.19, $p < 0.006$), suggesting we are missing the nonlinear signal in shorter time series.

Most time series describing biological populations contain a linear component convolved with a nonlinear component, and which component dominates depends critically on scale. For example, while individual cities in the UK exhibit highly nonlinear measles dynamics, when data are grouped for the country as a whole, the nonlinear signal disappears (as incoherent noise) because contact rates are dominated by uniform school openings and closures (Sugihara et al. 1990). Indeed, although the effects of scale should make the detection of nonlinearity difficult, the fact that nonlinearity is commonly observed in natural time series speaks to the dominance of the nonlinear signal when the correct scale is identified. Finally, for comparison, the degree of nonlinearity detected in these time series is comparable to that calculated for model output of a chaotic (intrinsic rate of increase, $r > 3.69$) logistic map with added noise (Hsieh et al. 2008). Thus, detecting nonlinearity can be subtle.

There is no definitive way to ground-truth abundance estimated from fishery-dependent catch and effort data; thus, there is no way to prove that these results reflect the "true" population dynamics of juvenile albacore (though we have proven that coherent and predictable CPUE dynamics exist). Nonetheless, in this case we feel confident that the nominal CPUE full-composite reflects the biological dynamics of the juvenile subpopulation. This is because at small spatial scales (e.g., the 1° × 1° cells used here), the fundamental premise underlying the use of CPUE as an index of abundance holds most true: that catchability is relatively constant (Hinton and Maunder 2004). In the case of these data, for which gear type, fishing nation, target species, and albacore age distribution are constant, the primary confounding variables are time (month, season) and space (latitude, longitude). By confining analysis of nominal data to disaggregated cells with constant space and season, we effectively standardize the data to these independent variables. Each observed time series in a given spatial cell therefore represents the change from year to year in the fish being caught in that cell, potentially describing changes in migration or habitat. However, when the data from individual cells are combined in the composite library, the model has information from the full region from which to build the best forecast. Because the data are not averaged or summed, analysis of the full region maintains the signal found at small spatial and annual time scales (through the construction of library and prediction vectors that are limited to consecutive points in a given cell) while describing the dynamics at the scale of the subpopulation.

As further support, the improvement in forecast skill and decrease in error found when comparing the target-composites to single series suggests the composite model is capturing dynamics that exist at a larger spatial scale than individual cells. The information contained in a library of 1365 cells, when combined, is better able to forecast the dynamics in a single cell than that cell is at forecasting itself. If the dynamic process was fundamentally different across cells in the region, the highest forecast skill should be achieved with the single cell analysis because historical data from that cell would produce the best forecasts. The qualitative similarity (low-dimensional, nonlinear)

Fig. 6. The use of composite libraries (target-composite analysis described in text) significantly improved the ability of the model to forecast a catch-per-unit-effort (CPUE) time series in a single cell compared with using the single cell to forecast itself. The target-composite also identified a higher embedding dimension (E) for the data. Marker is calculated mean, error bars are standard error. Improvement of target-composite over single series was calculated by two-tailed paired t test ($n = 39$; *, $p < 0.01$; **, $p < 0.001$). (*a*) Best E identified by simplex projection, (*b*) forecast skill (ρ) achieved by simplex projection, (*c*) ρ achieved by S-maps, (*d*) mean absolute error (MAE) of forecasts by S-maps.

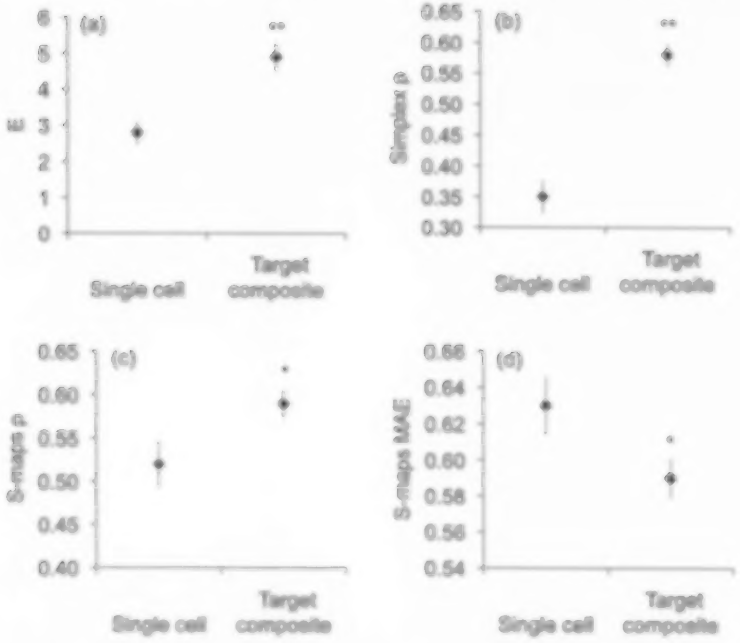
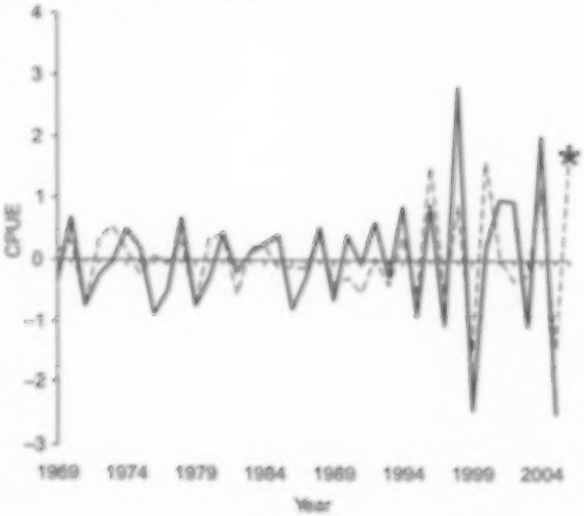


Fig. 7. The standardized catch-per-unit-effort (CPUE) time series from 1966 to 2005 was used to produce a forecast (*) for 2006. Simplex projection, the model producing the highest forecast skill, was used. Data were analyzed as normalized (mean = 0, standard deviation (SD) = 1) first differences. Solid line is observed data, dashed line is forecasted data.

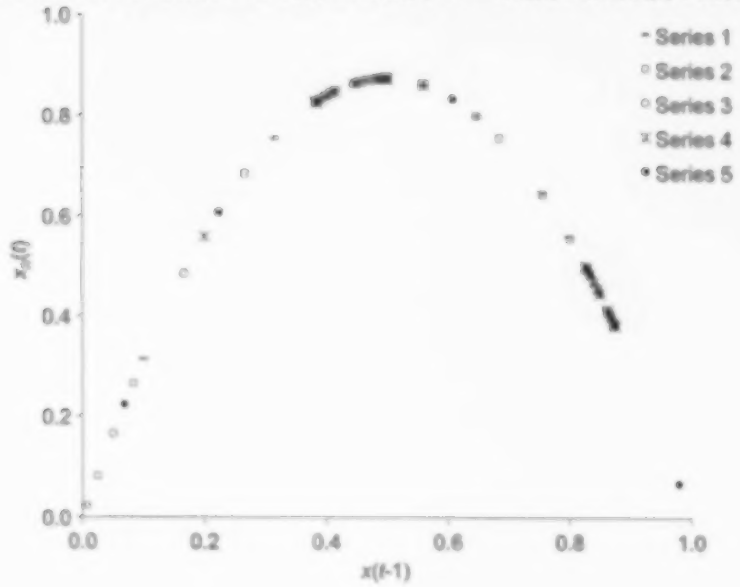


between the full-composite and mean values for the target-composites suggests the various configurations of scale converge on a coherent description of the data.

For nominal CPUE data, the application of composite methods overcomes challenges posed by short and incomplete time series. By combining many incomplete series, the model is more likely to find a sample of vectors long enough to test higher-dimension embeddings and the overall skill of the models is significantly higher. The composite approach also improves our ability to detect nonlinearity. Most (32 of 39) target time series contained at least one gap in the 40-year period. Of the seven complete time series, nonlinearity was detected in all of them. However, there was a 50% greater chance of detecting nonlinearity in the incomplete time series if a composite library was used. In summary, the repeated finding of nonlinearity in all complete single time series, nearly 50% of target-composites (with the accompanying higher forecast skill), in the full-composite and in the standardized data suggests the proper functional form is nonlinear.

For these data, the length of time series needed for skilful forecasts appears to be 33–35 years. Single cells containing 27 years of data were insufficient to identify nonlinearity, but those containing 33 years or more were identified as nonlinear. These findings are consistent with other studies comparing analysis of long and short time series using composite libraries, whereby forecasting of a known nonlinear model (even without observational noise) either did ($n = 150$ points) or did not ($n = 30$ points) detect that nonlinear-

Fig. 8. The logistic growth model ($x(t) = rx(t-1)[1 - x(t-1)]$) becomes increasingly defined as each of five time series (40 points long) is added. Many points cluster, but the occurrences of rare points add critical information about the full shape of the function. Likewise, compositing dynamically similar, but mutually exclusive, time series leverages spatially defined catch-per-unit-effort data, using what might otherwise be considered redundant. For the model, $r = 3.5$, $x_1(0) = 0.1$, $x_2(0) = 0.007$, $x_3(0) = 0.05$, $x_4(0) = 0.2$, $x_5(0) = 0.98$.



ity (Hsieh et al. 2008). Theoretically, the CPUE series with the most complete data (fewest gaps) correspond to areas of most regular fishing effort (and potentially highest fish abundance), making these cells likely to have lower observational noise than cells with incomplete series. Practically, the most complete time series also provide the model more information from which to build the attractor, as the neighborhood around the prediction vectors is denser.

Composite libraries add information to the reconstructed attractor that improves the model's ability to resolve forward trajectories or prediction vectors (Hsieh et al. 2008). In this study, the composite time series represent repeated samples or observations of the attractor describing the system in which albacore are harvested (samples of the process that are not identical). In the case of a multispecies composite (Hsieh et al. 2008), a time series provides a one-dimensional view of the attractor describing the community of interacting species. In the case of a single species composite, the individual time series can be thought of as iterations of the mechanistic model (e.g., a logistic population growth model) describing the fish population, but with different initial conditions (e.g., the (scaled) catch rate of fish in a cell at a given time). Each time series contributes information about the shape of the attractor; some of it is redundant, but some of it is new.

As a heuristic example, we demonstrate how the logistic population growth model (in canonical form), plotted as a two-dimensional embedding (also known as the logistic return map; May 1976), becomes more defined as successive, independent series with different initial conditions are plotted (Fig. 8). The parts of the function most densely filled with points represent values commonly observed (say, mean abundance levels, or in our case, mean catch rates). Such parts of the function are easily observed with only a few years of data from the first iteration. As points from less commonly observed parts of the function are added, critical (because they are rare) sections are filled in. In a similar fashion, the composite attractor created from 1366 time series spanning a large portion of the geographic distribution of juvenile albacore in the North Pacific includes information about the dynamics in areas of high catch rates (e.g., the time series in the CCS where albacore are densely aggregated and abundant), as well as in areas of low catch rates (e.g., in the migratory highway through the central gyre; Polovina et al. 2001). When combined, these time series produce a more defined attractor. Thus, this technique takes advantage of the large amounts of data available from spatially structured CPUE data sets to increase our ability to observe the full system attractor.

Analysis of the GLM-standardized time series presents two conclusions: data assimilation through standardization removes the nonlinear signal detected in the nominal data and reduces the complexity (dimensionality) of the dynamic process. Nonlinearity was detected only when the composite library of all cells (in nominal form) was used to forecast the standardized series. Furthermore, the GLM-single analysis found $E = 2$ as opposed to $E = 5$ with the composite (similar to the full-composite of nominal data). Given the goals of standardization, to reduce observation noise and remove the effects of confounding variables, this result is expected; the process of standardization effectively reduces the number of independent variables acting on the dependent variable, CPUE. For forecasting a standardized time series, the best model was simplex projection with an E of 2, using

the single series to forecast itself. The composite library did improve the forecast skill of S-maps, but the S-maps model produced less accurate forecasts than simplex projection.

This raises a critical point about the parameter E. As we use it here, E is not an absolute number that is intrinsic or invariant. Rather, the choice of E for a given model is operationally tied to the forecast skill that is practically achievable (given the amount of data and the observational noise). Embedding the time series in a given dimension produces a certain level of predictive skill that increases as the attractor is unwound, resolved so trajectories do not cross (i.e., singularities are resolved). Furthermore, while E can be thought of as corresponding to the axes in state space that affect the dependent variable (i.e., the critical driving variables in the system), there is not necessarily a one-to-one correspondence. In the case of our data, then, if the goal is to model the nominal time series, one would look for two to five variables to explain the system dynamics, with the aim of reproducing or surpassing the level of prediction skill attained with lagged coordinates. If the goal is to model the standardized time series, only two variables will be needed. The "missing" dimensions in the standardized series likely reflect the process of standardization itself. The difference between an E of 4 and an E of 5 is not the difference between a "correct" and an "incorrect" model. The important point is that the data sets can be modeled with relatively few dimensions.

This study provides a means of incorporating forecasts of time series containing nonlinear dynamics into stock assessment models and of supplementing current approaches to management. Most stock assessment models make forecasts, sometimes 10 years into the future, based on an equilibrium state estimated from historical data and with an additive stochastic component to replicate recruitment variability (for albacore, see Stocker 2005; ISC 2007). The population dynamics model is then evolved in time based on static coefficients, and the resulting biomass forecasts become asymptotic. Instead of basing the stock assessment forecast on stable dynamics, here we suggest that an annual CPUE forecast be used to drive the stock assessment model either by predicting catch rate for each individual cell or by predicting the trajectory of the standardized series. This would be particularly valuable for short-lived species (such as pollock (*Pollachius virens*) or Pacific cod (*Gadus macrocephalus*)) for which total allowable catch is updated every year based on annual assessments. Stock assessment models also produce short-term forecasts that could be directly compared with the output of our models. While the nonlinear methods do not make predictions many years into the future, for the purpose of management, 1-year-ahead forecasts are an important product. For species that are longer lived and where constant mortality assumptions are valid, these forecast methods can be used on annual recruits and extrapolated upward to create longer-term forecasts for the stock.

Equilibrium-based models of fisheries could fail to predict major population changes (Mangel et al. 2002). Nonlinear models, especially ones like these that are not constrained by distributional assumptions for variables such as mortality or spawner–recruit relationships, may provide more accurate (yet simpler) ways of modeling the dynamics of populations. Such flexibility in the model also overcomes structural uncertainty inherent in traditional population dynamics models. The choice between data models and algorithmic models does not have to be zero-sum (Breiman 2001); we advocate the use of both types of models to maximize biological understanding and forecast accuracy and to provide a means of validation. Finally, data compositing methods offer a technique complementary to standardization for analyzing CPUE data that is directly useful in management of marine fisheries. Both the composite analysis and the GLM are means of assimilating large amounts of data into a single estimate of stock size.

This approach is not a silver bullet for stock assessments. Most notably, in its current univariate form, forecasts are not provided as a function of varying levels of effort, a necessary feature when setting harvest guidelines (although effort changes can be accommodated with a multivariate approach; Dixon et al. 1999). Consequently, we see the information obtained from these methods as complementary to that obtained from stock assessment models that can produce proscriptive recommendations based on varying levels of catch or effort. Our approach makes distribution-free forecasts in a way that allows analysis of error in the model, but also captures the dynamic signature underlying the data and provides insight into the degree of complexity underlying the processes governing albacore dynamics.

In summary, the juvenile subpopulation of North Pacific albacore display low-dimensional, weakly nonlinear dynamics that can be forecast 1 year ahead. We add a new method to the suite of fisheries models that accounts for the nonlinear structure of natural populations and can be used to overcome limitations posed by short and incomplete CPUE time series. Further, we suggest that large data sets containing highly resolved, spatially structured CPUE data should not be treated as though individual time series contain only redundant information to be assimilated and averaged. Rather, such time series, even those on the geographic periphery of the species' range, contain valuable information about the dynamic structure of the population. The large data set available for North Pacific albacore demonstrates the usefulness of such a suite of data. Given the ability of low-dimensional nonlinear models to forecast changes in albacore CPUE, forecasts made at the level of CPUE time series should supplement those made by stable population dynamics models. Such an addition to current stock assessments will provide a baseline for active management of the population, indicators of (potentially important) future changes to population abundance, and a template for forecasting key subprocesses such as recruitment.

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Identifying nonproportionality of fishery-independent survey data to estimate population trends and assess recovery potential for cusk (*Brosme brosme*)

Trevor D. Davies and Ian D. Jonsen

Abstract: Cusk (*Brosme brosme*) was designated as "threatened" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in 2003, based on an estimated 93% decline between 1970 and 2001 from the Fisheries and Oceans Canada (DFO) Scotian Shelf summer bottom trawl survey index. We combined this index with a fishery-dependent longline index in a Bayesian surplus production state-space model to estimate population trends and the recovery potential of western Scotian Shelf cusk. We tested for index nonproportionality using a power curve function in the observation model and identified potential hyperdepletion for cusk in the trawl survey index. We estimate a 59% decline in cusk biomass between 1970 and 2001, and a 64% decline from 1970 to 2007. Although population projections indicate the current landing limit should lead to population recovery, robustness tests suggest the biomass projections and recovery time lines are overly optimistic. Simulations showed that incorporating multiple indices increases power to recapture model parameters and failure to account for index nonproportionality results in biased parameter estimates. We suggest that nonproportionality of fishery-independent indices must be considered when determining the population status of data-poor species.

Résumé : Le brosme (*Brosme brosme*) a été désigné espèce menacée par le Comité sur la situation des espèces en péril au Canada (COSEPAC/COSEWIC) en 2003 en se basant sur un déclin estimé de 93 % de 1970 à 2001 d'après l'indice de l'inventaire par chalutage de fond en été sur la plate-forme Néo-écossaise de Pêches et Océans Canada (MPO/DFO). Nous combinons cet indice avec un indice basé sur la pêche commerciale à la palangre dans un modèle bayésien état-espace de production excédentaire afin d'estimer les tendances de la population et le potentiel de récupération des brosmes de l'ouest de la plate-forme Néo-écossaise. Nous avons vérifié l'absence de proportionnalité de l'indice à l'aide d'une fonction de courbe de puissance dans le modèle d'observation et avons décelé un épuisement exagéré dans l'indice basé sur l'inventaire au chalut. Nous estimons un déclin de 59 % de la biomasse des brosmes de 1970 à 2001 et un déclin de 64 % de 1970 à 2007. Bien que les projections démographiques indiquent que la limite actuelle des débarquements devrait permettre une récupération de la population, des tests de robustesse montrent que les projections de biomasse et les échéanciers de récupération sont trop optimistes. Des simulations révèlent que l'incorporation de plusieurs indices augmente le pouvoir de récapture des paramètres du modèle et que la négligence de l'absence de proportionnalité des indices entraîne une erreur dans l'estimation des paramètres. Nous suggérons qu'il est nécessaire de tenir compte de l'absence de proportionnalité dans les indices indépendants de la pêche quand on détermine le statut d'espèces pour lesquelles on possède peu de données.

[Traduit par la Rédaction]

Introduction

Fisheries stock assessments are frequently based on data intensive population dynamics models, and thus are generally limited to the target species of large-scale commercial fisheries (Davis 2002; Kelly and Codling 2006). On the east coast of Canada, for example, stock assessments have been conducted for fewer than 5% of all marine fish species (Hutchings and Baum 2005). Detailed life-history information and appropriate long-term catch and monitoring data required for such assessments are typically lacking for incidentally caught species (McAllister et al. 2001; Hall and Mainprize 2005). These species may, however, experience significant incidental mortality as bycatch (Crowder and Murawski 1998; Baum et al. 2003), and it is therefore essential that quantitative estimates of the impacts of exploitation on them are developed.

Cusk (*Brosme brosme*) is a data-poor benthic teleost (Family Gadidae) of the north Atlantic, which is commonly

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caught as bycatch in benthic longline and lobster fisheries (DFO 2004). Little is known about its life history and ecology; however, catch rates in eastern Canada's groundfish longline fishery suggest cusk prefer rocky complex habitat in relatively deep water (400–600 m, Oldham 1966; Harris et al. 2002). Life history parameters including growth rate, natural mortality, and maximum age are unknown. Cusk is principally a bycatch species in Canada and the US, but is frequently retained prior to landing limits being reached. In Canada, landings were unregulated until 1999, after which a limit of 1000 t was imposed for the majority of the Scotian Shelf (4VWX Northwest Atlantic Fisheries Organization (NAFO) divisions). Owing to increased conservation concerns, this limit was reduced to 750 t in 2003 and extended to include the Canadian portion of Georges Bank (5Zc, DFO 2008).

Cusk was designated as "threatened" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in 2003, based on an estimated 93% decline between 1970 and 2001 in the Fisheries and Oceans Canada (DFO) Scotian Shelf summer bottom-trawl survey index (COSEWIC 2003). This estimate has been contested by DFO scientists because the trawl survey samples outside the preferred habitat and depth range of cusk, and therefore, the survey index may not be proportional to cusk population abundance (DFO 2004). The assumption that catch rate indices are proportional to abundance is commonly made in population models, and was used in the COSEWIC assessment, despite the fact that it rarely holds (Richards and Schnute 1986; Harley et al. 2001; Maunder et al. 2006). Nonproportionality has been recognized to occur in commercial catch-rate data (Harley et al. 2001); however, fishery-independent data can also suffer from nonproportionality if a large component of the stock is found outside the survey area (Blanchard et al. 2008). Failure to account for nonproportionality when present, in either commercial catch rate or fishery-independent data, can result in biased estimates of stock decline.

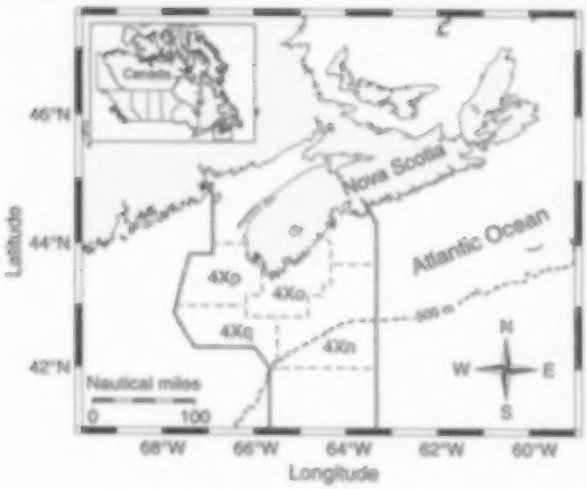
The objectives of our research were to estimate historical population trends, current status, and the recovery potential of western Scotian Shelf cusk (NAFO division 4X; Fig. 1) by using two indices of relative biomass and evaluating each of them for nonproportionality. We incorporated a fishery independent bottom-trawl survey index and a fishery dependent catch-per-unit-effort (CPUE) benthic longline index within a Bayesian state-space surplus production model, and used a power curve function in the observation model to test for nonproportionality of the indices. We then used the model-derived biomass and parameter estimates in stochastic simulations to project biomass forward and assess recovery potential based on three different landing limits. Finally, we used a simulation approach to evaluate consequences of model misspecification and the advantages of using both indices to obtain unbiased parameter estimates.

Materials and methods

Data

Time-series data for cusk on the western Scotian Shelf include annual reported landings and two catch rate indices of relative biomass (Fig. 2). One index is a fishery-independent

Fig. 1. Location of study. Bold unbroken line is the 4X major Northwest Atlantic Fisheries Organization management unit area. Dashed lines are the minor management units from which the commercial longline index is derived. Ragged dashed line is the 500 m isobath.

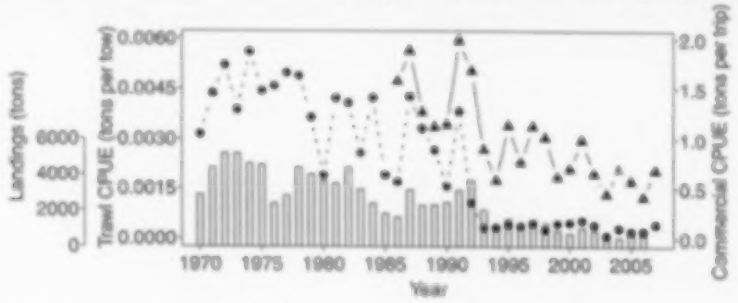


index based on the DFO summer bottom-trawl survey, and the second is a fishery-dependent index derived from the commercial groundfish longline fishery, in which cusk is bycatch. Owing to insufficient data on unreported and incidental mortality, we make the assumption that reported landings are synonymous with fishery removals and are known without error. The DFO summer bottom-trawl survey covers most of the Scotian Shelf and has been conducted each July since 1970. The survey follows a stratified random design with stratification based on depth and geographic area (Shackell and Frank 2003). The stratified mean catch per standard 1.75 nautical mile tow (1 international nautical mile = 5.56 km) is used as an index of relative biomass. We restricted the index to only include the western Scotian Shelf (4X NAFO division) so that it would cover the same region as the commercial catch rate index. Cusk catch rates in the survey have always been low because the rocky complex habitat preferred by cusk (Oldham 1966) is poorly sampled by the survey trawl gear.

The CPUE index from the commercial groundfish longline fishery covers most of the western Scotian Shelf (4Xnopq NAFO subdivisions) and spans from 1986 to 2007. We focused on this fishery because it has the highest cusk catches in Atlantic Canada (>95% of all cusk landings on the Scotian Shelf and Georges Bank since 1990). Catches from areas of marginal cusk habitat, such as the Bay of Fundy and shallow inshore regions, were not included. The index was restricted to vessels of 25 to 149.9 gross registered tons, since no effort information was available for smaller longliners in early parts of the time-series. To avoid introducing bias from landing limits being reached, we restricted the commercial catch rate index to the first 3 months of each year's fishing season (July to September).

Reported landings and the commercial index may be biased high in the time series.. The lack of a landings limit for cusk prior to 1999 could, for example, have resulted in

Fig. 2. Time-series of fishery independent bottom trawl (filled circle, ●), and commercial longline catch-per-unit-effort (filled triangle, ▲) indices for cusk from the 4Xnopq NAFO subdivisions. Recorded landings (bars) are from the 4X NAFO division.



target-species such as cod (*Gadus morhua*) being reported as cusk when cod quotas were exceeded, thus potentially inflating the cusk landings and commercial catch rates. Because the level of misreporting could not be quantified, we did not apply corrections to either time series. However, the level of misreporting, if present, in the longline fishery index prior to 1999 appears minor, as the index follows the yearly catch rate dynamics in the fishery-independent trawl index over the same period (Fig. 2).

The lack of age or length disaggregated data for both indices limited our choice of population models and our ability to track year class variability and population age-structure. Although age and length disaggregated information exists for the trawl survey time-series, commercial data was limited to yearly biomass and effort, and landings simply as biomass. If catch-at-age/length data were available for all the data series, we could have compared the catch rates of each size class over time to better understand the relationship of each time-series to population abundance.

Population model

Recognition of the importance of both observation error and process variability has increased the application of state-space models in the assessment of fish and endangered species in the last decade (Harwood and Stokes 2003; Clark and Bjørnstad 2004). State-space models differ from traditional deterministic population models in that they consist of two components: a process model, which represents the unobservable stochastic processes governing the population dynamics, and an observation model, which describes the error structure inherent in the observations (Meyer and Millar 1999*b*; Harwood and Stokes 2003). By coupling these components in a state-space framework, the errors in the observations can be separated from natural variability in the population processes. We employed a Schaefer surplus production model (Schaefer 1954) as our process model, because there was insufficient age-disaggregated and life history data to use more complex age-structured models. Surplus production models are commonly employed when indices of relative biomass and landings are the only data available for population assessment (Hilborn and Walters 1992). Implicit assumptions of the Schaefer model are a symmetrical surplus production curve where maximum surplus production (MSP) occurs at 50% of unfished biomass, and a population at equilibrium (Schaefer 1954; Hilborn and Walters 1992). The Schaefer surplus production model is

$$(1) \qquad B_t = \left(B_{t-1} + rB_{t-1}\left(1 - \frac{B_{t-1}}{K}\right) - C_{t-1}\right)\eta_t$$

where B_{t-1} and C_{t-1} denote biomass and catch (landings), respectively, for year t–1. Carrying capacity, K, is the biomass of the population at equilibrium prior to commencement of the fishery; r is the intrinsic population growth rate; and η_t is a lognormal random variable with a mean of zero and variance σ^2 to account for stochasticity in the population dynamics. Recruitment, growth, and natural and unreported fishing mortality are combined in the time-invariant parameter, r. All parameters are held constant over time (i.e., changes in the biotic and abiotic environment are not included) and catchability is the same for all individuals in the population.

The observation model relates the unobserved states, B_t, to the indices of relative biomass, $I_{i,t}$, that are observed with error. We incorporate both the trawl survey index and longline index in a single model by specifying a separate observation equation for each. A commonly used observation model is

$$(2) \qquad I_{i,t} = q_i B_t \varepsilon_{i,t}$$

where $I_{i,t}$ is the relative abundance of index i at time t; q_i is the catchability coefficient for index i, which describes the effectiveness of each unit of fishing effort; and $\varepsilon_{i,t}$ is a lognormal random variable with a mean of zero and variance τ_i^2 to account accounting for error in the observations of index i.

A critical assumption of eq. 2 is that the catch rate indices are assumed to be proportional to biomass, regardless of population size (i.e., constant q). Because our data are spatially aggregated and have no age-disaggregation, the catchability parameter is a conglomeration of the three different processes governing the effectiveness of the fishing gear: availability, catchability, and selectivity. Density dependent habitat selection exhibited as range contraction to optimal habitat areas as abundance declines is observed in many exploited fish stocks (Blanchard et al. 2008). We hypothesize that as cusk biomass declined, remaining individuals retreated to optimal habitat areas where they remained available to the longline fleet but were less available to trawl gear, which is restricted to noncomplex substrate that is con-

sidered to be poor cusk habitat. Unfortunately, spatially disaggregated catch rate data for the commercial fleet was unavailable to directly test this hypothesis. Rather, to account for this potential change in cusk availability to the trawl gear, we relaxed the assumption of constant catchability by adding a shape parameter to the observation model. This power curve relationship between the catch rate indices and population biomass allows catchability to change as population biomass changes. Catchability then becomes a function of q and β (catchability = $qB^{\beta-1}$, Harley et al. 2001). Our observation model becomes eq. 3:

$$(3) \qquad I_{i,t} = q_i B_t^{\beta_i} \varepsilon_{i,t}$$

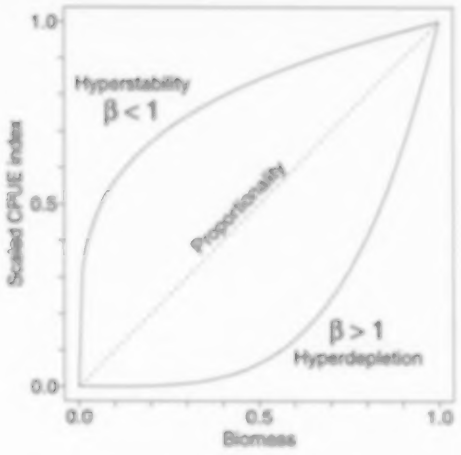
where β_i is a shape parameter for index i.

Equation 3 reduces to eq. 2 when $\beta = 1$. In the context of population declines, $\beta < 1$ implies the catch rate index declines more slowly than population biomass, a condition known as hyperstability (Fig. 3). Hyperstability occurs in many commercial catch rate indices (Harley et al. 2001) and can be the result of the nonrandom search behaviour of fishers and (or) schooling behaviour or range contraction of target species (Rose and Kulka 1999). Assuming proportionality of a hyperstable index can result in underestimates of exploitation rate and total population decline (Hilborn and Walters 1992). Conversely, hyperdepletion occurs when $\beta > 1$ and describes the situation where the catch rate declines faster than population biomass (Fig. 3). This can occur when fishing effort is concentrated on a subset of the population that may be depleted, while a significant subset of the population remains unaccounted for in the catch rate index (Quinn and Deriso 1999). For example, the fixed area design of fishery-independent surveys can potentially result in a hyperdepleted catch rate index if the core density of a species is outside the survey area and species specific processes such as density dependent habitat selection results in incomplete mixing of the population within its full range (Blanchard et al. 2008). Assuming a hyperdepleted index is proportional to biomass can result in overestimates of population decline and exploitation rate (e.g., Myers and Worm (2003) as pointed out by Walters (2003), Maunder et al. (2006) and Sibert et al. (2006)).

Four variants of the observation component of the surplus production model were compared: (*i*) both indices fixed to be proportional to biomass (i.e., $\beta = 1$); (*ii*) shape parameters estimated for both indices; (*iii*) the longline index fixed to be proportional to biomass and a shape parameter estimated for the trawl index; and (*iv*) the trawl index fixed to be proportional to biomass and a shape parameter estimated for the longline index.

We implemented the state-space models in WinBUGS (version 1.4.3, Lunn et al. 2000) via the R2WinBUGS package (Sturtz et al. 2005) in the statistical programming environment R (R Development Core Team 2008). WinBUGS uses a Markov Chain Monte Carlo (MCMC) approach to estimate the joint posterior distribution of the model parameters. Marginal posterior distributions of model parameters and unobserved states were based on 300 000 iterations of two chains after discarding the first 260 000 iterations (burn-in). These 40 000 iterations were reduced to 2000 by sampling every 20th value to reduce sample autocorrelation. Models were considered to have converged when the potential scale reduction factor $\hat{R}$ was <1.2 for all parameters (Brooks and Gelman 1998). See online supplementary data[2], Appendix S1 for WinBUGS code.

Fig. 3. Three possible power curve relationships of catch-per-unit-effort and biomass. Figure adapted from Hilborn and Walters (1992).



Priors

A potential advantage of the Bayesian approach is that other sources of information can be incorporated into the analysis in the form of priors (Gelman et al. 2004). Unfortunately, since little is known about cusk ecology or its catchability on trawl or longline gear, we were limited to relatively broad flat priors (Table 1). We specified a vague prior for carrying capacity, K, using a uniform distribution with a lower boundary of the maximum reported landings of 5219 t and an upper boundary of 500 000 t. Although the upper boundary is greater than reasonable predictions for K, it was used to ensure that some probability density would be present in unlikely, although possible estimates of K. The purpose of this prior was to restrict the parameter search away from mathematically possible yet biologically implausible parameter combinations (e.g., a high estimate for r coupled with an extremely low estimate for K). We made the assumption that the cusk population at the beginning of the trawl index (1970) was equal to K with an error distribution equal to the estimated process error, because the trawl catch rate was relatively stable from 1970 to 1980, and estimating, rather than specifying B_0, increases confounding in the model parameters (Hilborn and Walters 1992). Furthermore, the low contrast and "one-way-trip" trends exhibited by both the survey and commercial data make estimating B_0 as a free parameter difficult. Estimates of absolute decline therefore need to be viewed in the context of this assumption.

We considered including an informative prior for the shape parameter, β. Harley et al. (2001) obtained maximum-likelihood estimates of shape parameters for commercial

[2] Supplementary data for this article are available on the journal Web site (http://cjfas.nrc.ca).

Table 1. Summary of specified priors for Bayesian state-space model.

Parameter	Prior
r (intrinsic growth rate)	Uniform(0,4)
K (carrying capacity; tons)	Uniform(5219, 500 000)
σ^2 (process error variance)	Uniform(0, 100)
τ^2 (observation error variance)	Uniform(0, 100)
q (catchability coefficient)	Uniform(0,1)
β (shape parameters)	Uniform(0.01,10)

catch rate indices of flatfish, cod, and other gadiformes, and found strong evidence of hyperstability in many indices. This property likely arose because of the searching and targeting behaviour of fishers for these target species (Hilborn and Walters 1992). We did not incorporate their findings into our analyses because cusk is taken primarily as bycatch, and there was weak a priori reason to expect hyperstability in the commercial catch rate index.

Model selection and sensitivity

We used two methods for model selection and to evaluate model fit. First, we utilized the estimated deviance information criterion (DIC), which penalizes model complexity and a lower score identifies a better model fit. Second, we conducted a retrospective analysis by omitting the last 7 years of the biomass indices (but retained the landings data) and checked the model's ability to predict the missing data by projecting the model forward 7 years (e.g., Gelman et al. 2004; Snover 2008). The decision to omit 7 years was largely arbitrary; however, we felt that 7 years was a good balance between retaining enough data for representative model fits and evaluating the predictive ability of the model. We used this approach to determine how well each model could predict future states and to assess the robustness of the parameter estimates. This approach also had the added benefit of evaluating the robustness of the recovery scenarios under different future catch rates. Lastly, we evaluated the sensitivity of parameter estimates to alternative specifications of the r and error variance priors for the model that received the most support according to the two criteria described above to ensure that the Bayesian analysis was not driven by the priors (McAllister et al. 2001). Therefore, we re-fit Model 3 with either lognormal priors with a mean of 0.25 or 1.0 and a variance of 1.0 for r and normal priors with a mean and variance of 1.0 for the process and observation error variances (σ^2, τ_L^2, and τ_T^2).

Biomass projections

Biomass was projected into the future to evaluate whether the current landing limit of 750 t is sufficient to allow for population recovery. Because the error associated with the observation process has no effect on the true population biomass, the state-space approach can be particularly useful when generating biomass projections using model derived population parameters. Indeed, if observation error is significant, and simply combined with process error, the uncertainty of population projections can be overestimated and potentially biased (Dennis et al. 2006).

Three catch landings levels were evaluated: 0, 750, and 1500 t per year. Projections were done in R using a stochastic simulation approach with the retained MCMC parameter realizations (B_{2007}, r, K, σ) from the joint posterior probability distribution of the model that assumed the longline index was proportional to biomass but estimated a shape parameter for the trawl index (Model 3 because this model received the most support according to the criterion described above). We changed modeling platforms for the projections due to the lack of programming flexibility in WinBUGS and because the lognormal distributional assumption of the population in the retrospective model can become invalid at unsustainable specified catch levels. We generated five process error deviated biomass realizations per year using the retained associated parameter realizations (n = 4000 after burn-in and thinning; for a total of 20 000 biomass estimates per year). Population realizations were fixed to zero once they became extinct.

The equilibrium assumption of the Schaefer model means that a change in exploitation rate will result in an immediate change in the population growth rate, thus potentially omitting important ecological processes such as recruitment time-lags and changes in population growth rate resulting from an altered age structure. Consequently, projections will likely overestimate biomass increases in response to reductions in fishing mortality.

Simulations

We used a simulation approach to investigate the consequences of model misspecification on the parameter and biomass estimates, and to quantify the advantage of including both indices of relative biomass, rather than just one (Table 2). To retain features of our best estimates of the true biomass trajectory, the landings data, and index histories for this particular stock, we employed a method akin to a parametric bootstrap by taking the median biomass estimates obtained from Model 3 as the true biomass trajectory for our simulations. We created our simulated indices of relative biomass (spanning 1970 to 2007 and 1986 to 2007 for the simulated trawl and longline indices, respectively) by multiplying the median yearly biomass estimates by the estimated catchability coefficients for each index. We generated two indices for the trawl index, one that was proportional to biomass, and a hyperdepleted index that had a power curve relationship with a defined shape parameter of β = 2.5. Small amounts of observation error (τ = 0.1) were added to each index for efficient MCMC sampling. We kept the observation error low as we wanted to observe the effects of model misspecification on the parameter estimates and not have the results obscured by noise in the observation process. To aid in comparison between models, the same random seed was used to generate observation noise for the proportional and nonproportional trawl indices.

Results

Model summaries and trends

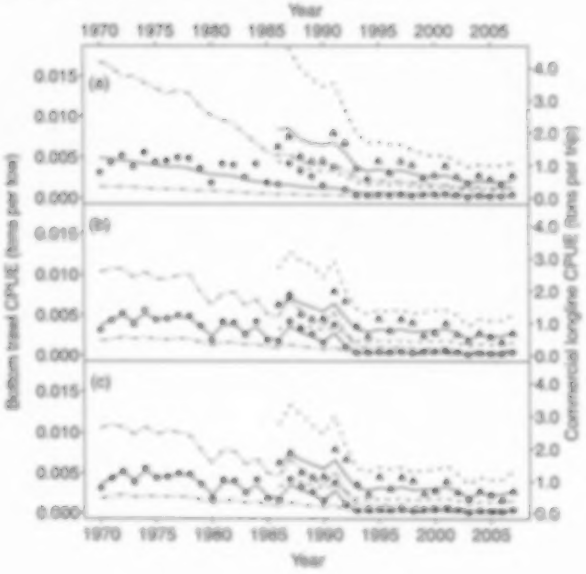
In all four models, posterior distributions for r and K were correlated and had a strong positive skew. Both of these features were expected, as r and K are frequently confounded in a Shaefer model (Haddon 2001) and the positive skew arises from the defined lognormal distribution of the biomass parameter. Regardless, all models passed convergence

Table 2. Summary of data and scenarios used for simulation evaluation.

		Data			
Scenario ID	Model assumptions	$P_{longline}$	P_{trawl}	S_{trawl}	Landings
Model 3	Parameter estimates from Model 3	—	—	—	—
A	Trawl survey assumed proportional		✔		✔
B	Trawl survey assumed proportional			✔	✔
C	Longline index assumed proportional	✔			✔
D	Both indices assumed proportional	✔	✔		✔
E	Both indices assumed proportional	✔		✔	✔
F	Both indices assumed nonproportional	✔		✔	✔
G	Trawl survey assumed nonproportional & longline index assumed proportional	✔		✔	✔

Note: Two simulated trawl indices were created, one that is proportional to biomass (P_{trawl}), and another that is hyperdepleted and follows a power curve ($\beta = 2.5$; S_{trawl}). Both span from 1970 to 2007. The simulated longline series is proportional to biomass and spans 1986 to 2007 ($P_{longline}$).

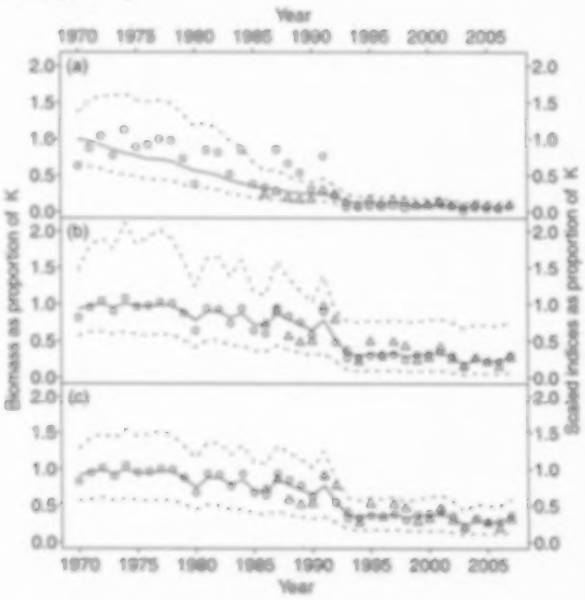
Fig. 4. Surplus production model fits to commercial longline catch-per-unit-effort (filled triangles, ▲) and fishery-independent bottom trawl (filled circles, ●) indices. Panel (*a*) assumes both indices are proportional to biomass (Model 1). Panel (*b*) estimated shape parameters (β_i) in the observation equation for both indices (Model 2). Panel (*c*) is fit of model assuming commercial longline index is proportional to biomass and estimates a shape parameter for the bottom trawl survey (Model 3). Unbroken and broken lines are median and 95% credible limits, respectively.



diagnostics. Model 1, in which both indices were defined to be proportional to biomass, did not fit the data well. This is evident by the lack of fit to the trawl index early in the time series and the underfitting during the transition period of high to low biomass in the early 1990s (DIC, –436; Fig. 4*a* and Fig. 5*a*). The model accounted for the lack of fit by estimating a large observation error variance (τ_T^2) for the trawl index (Table 3). Posterior density plots indicated that there was sufficient information to estimate the r and K parameters (Figs. 6*a* and 6*b*).

Estimating shape parameters for both indices (Model 2) improved the model fit (Fig. 4*b*; DIC, –522). The credible

Fig. 5. Biomass as proportion of carrying capacity (B_t/K) estimates from surplus production model fit to commercial longline catch-per-unit-effort (open triangles, Δ) and fishery independent (open circles, ○) bottom-trawl indices. Panel (*a*) assumes both indices are proportional to biomass (Model 1); Panel (*b*) Estimated shape parameters (β_i) in the observation equation for both indices (Model 2); Panel (*c*) is fit of model assuming commercial longline index is proportional to biomass and estimates a shape parameter for the bottom trawl survey (Model 3). Observations have been scaled, where appropriate, by the estimated catchability coefficient ($q_{longline}$; q_{trawl}) and shape parameter(s) ($\beta_{longline}$; β_{trawl}) for each index. Unbroken and broken lines are median and 95% credible limits, respectively.



limits of the biomass estimates contained all of the scaled index values. The credible limits were also substantially wider than in Model 1, owing to the increased uncertainty in K (Fig. 5*b*). The median of the posterior for r, although slightly smaller, was similar to Model 1 and credible limits were slightly larger. Conversely, the median of the posterior for K was slightly larger, but the upper 95% credible limit was almost double that estimated by Model 1 (Table 3).

Table 3. Summary of posterior quantiles of parameters for Models 1, 2 and 3.

	Model 1			Model 2			Model 3		
Parameter	2.5%	Median	97.5%	2.5%	Median	97.5%	2.5%	Median	97.5%
Intrinsic rate of pop. growth (r)	0.015	0.149	0.505	0.007	0.126	0.555	0.007	0.115	0.362
Carrying capacity (K; tons)	24 750	53 270	126 708	20 480	57 225	232 605	24 399	51 580	192 013
Biomass in 1970 (B_{1970}; tons)	22 477	53 670	124 902	14 810	53 900	235 223	18 470	47 430	190 718
Biomass in 2007 (B_{2007}; tons)	1721	4204	10 440	2248	15 565	137 713	5371	16 900	85 271
B_{1970}/K	0.67	1.00	1.37	0.57	0.93	1.46	0.57	0.91	1.28
B_{2007}/K	0.04	0.08	0.15	0.07	0.29	0.76	0.14	0.34	0.58
Longline catchability (q_L)	5.1×10^{-5}	1.3×10^{-4}	3.1×10^{-4}	8.0×10^{-5}	3.6×10^{-4}	1.2×10^{-3}	8.9×10^{-6}	4.2×10^{-5}	1.3×10^{-4}
Trawl catchability (q_T)	3.8×10^{-8}	9.4×10^{-8}	2.3×10^{-7}	1.5×10^{-8}	8.4×10^{-8}	3.6×10^{-7}	1.6×10^{-8}	9.6×10^{-8}	4.0×10^{-7}
Process error variance (σ^2)	0.00	0.02	0.14	0.00	0.04	0.25	0.01	0.03	0.09
Longline Obs. error variance (τ_L^2)	0.02	0.09	0.27	0.03	0.06	0.14	0.03	0.06	0.14
Trawl Obs. error variance (τ_T^2)	0.18	0.32	0.57	0.00	0.09	0.26	0.00	0.08	0.27
Shape parameter for longline	—	—	—	0.35	0.83	3.49	—	—	—
Shape parameter for trawl	—	—	—	1.00	2.06	8.61	1.62	2.48	3.60
Max. surplus prod. (MSP; tons)	340	2005	4012	153	1846	6486	142	1538	5281
Biomass giving MSP (B_{MSP}; tons)	12 380	26 635	63 373	10 240	28 615	116 302	12 200	25 790	96 025
B_{2007}/B_{msp}	0.08	0.15	0.31	0.14	0.58	1.52	0.27	0.68	1.16
DIC		–436			–522			–577	

Observation error for both indices was smaller than Model 1, and the estimated observation error for the trawl index was larger than the longline index. Although there was overlap in the posterior densities of the shape parameters, both were identifiable and the modes of the posterior densities were well separated (Fig. 6*i*). The median estimate for the longline index shape parameter was 0.83; however, about 62% of the probability density of the posterior was less than 1.0, which suggests weak evidence that the index is hyperstable. Conversely, the median estimate for the trawl index shape parameter was 2.06, and 97.5% of the probability density was greater than 1.0 suggesting substantial hyperdepletion in the trawl index. The results from Model 2 suggested that a more parsimonious model, in which a shape parameter is estimated for the trawl index only, would result in a comparable model fit, and indeed Model 3, with one less parameter, had the most support (DIC, –577). Model fit to the observations was similar to Model 2 (Fig. 4*c*); however, yearly biomass estimates had tighter credible limits and still contained all scaled trawl and longline index values (Fig. 5*c*). Estimates of observation error for both indices were virtually identical to Model 2. The range of uncertainty in K was greater compared with Model 1, but less so than Model 2. In contrast, the credible limits of r were much more narrow, yet the median estimate was similar to both Model 1 and 2. The model estimated greater hyperdepletion in the trawl index compared with Model 2, and the posterior of the estimated shape parameter was well defined and had less skew (Fig. 6*n*). We estimate a 59% decline in cusk biomass between 1970 and 2001, a 64% decline from 1970 to 2007, and estimate stock biomass to be at 68% of maximum surplus production under Schaefer model assumptions (MSP, Table 3) in 2007.

Model 4, in which a shape parameter was estimated for the longline index only, had the least support of all shape parameter models (DIC, –497). Severe hyperstability was estimated in the longline index (median, 0.41) and process error was substantially larger than all other shape models (plots not shown).

Model sensitivity

We evaluated the robustness of the model fits and parameter estimates for Models 1 to 3, and further tested Model 3 against alternate forms of the r prior. Omitting the last 7 years of data had little effect on the estimated parameters; however, the predicted observations for both indices were all greater than the omitted data for all models (Fig. 7). Alternate forms of the r prior for Model 3 had relatively little effect on either the model fit or parameter estimates. Indeed, the more informative of the alternate lognormal priors, which had a mean and variance of 1.0, only changed the median posterior estimate of r from 0.115 to 0.122 (95% credible limits of 0.03–0.35), which is very similar to the original Model 3 that had a flat r prior (Table 3). Similar minor changes to the parameter estimates were observed when we replaced the flat priors with informative normal priors with a mean and variance of 1.0 for σ^2, τ_L^2, and τ_T^2. The median estimates for Model 3 became as follows: r, 0.124; K, 48 075; σ^2, 0.036; τ_L^2, 0.064; and τ_T^2, 0.085, which are very close to those estimated when flat priors were used (Table 3).

Fig. 6. Posterior density plots of select model parameters. Where separate parameters are estimated for each data series, the commercial longline catch-per-unit-effort index is described by a grey line and the fishery-independent trawl survey a black line. Priors are identified as broken lines. (*a*) Model 1 (panels *a*–*d*) assumed both indices were proportional to biomass, (*b*) Model 2 (*e*–*i*) estimated a shape parameter for both indices; and (*c*) Model 3 (*j*–*n*) estimated a shape parameter for the trawl survey only.

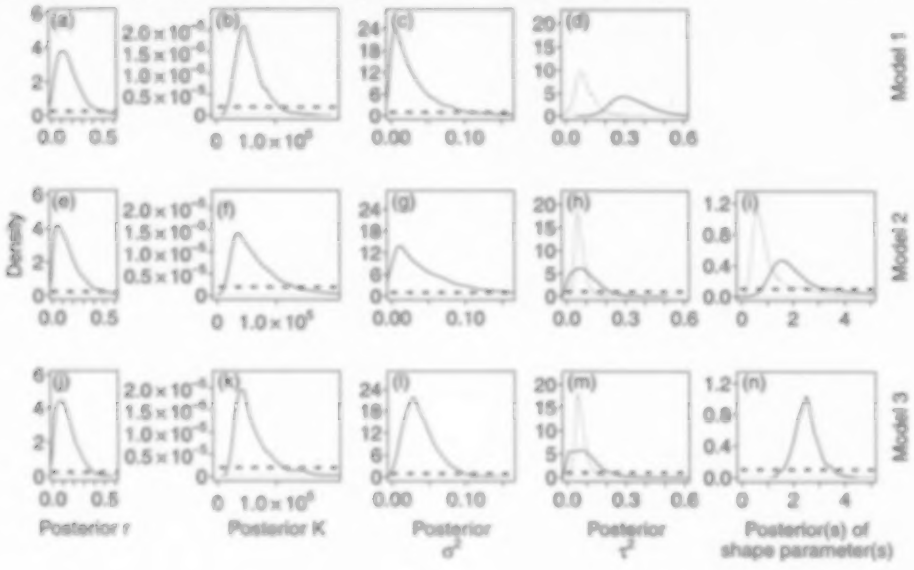
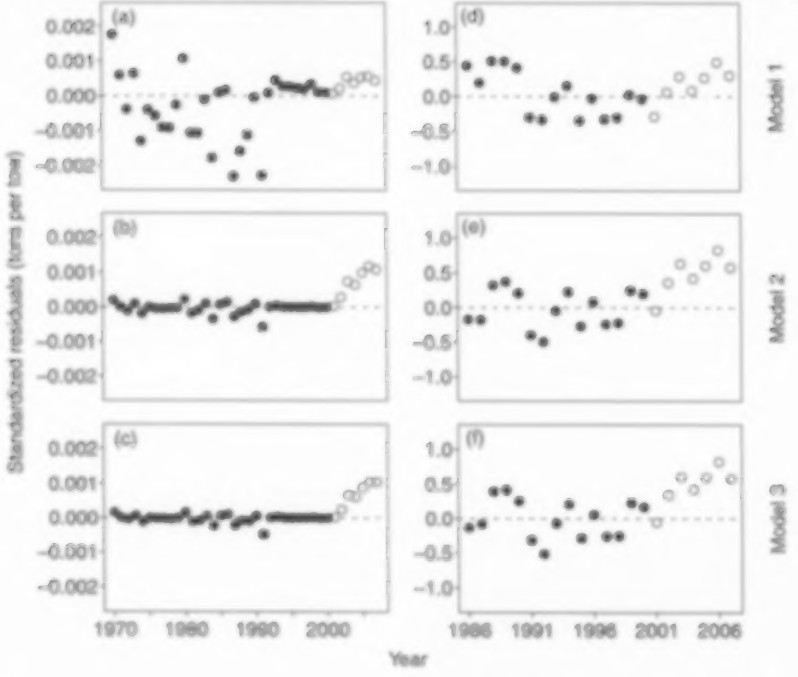


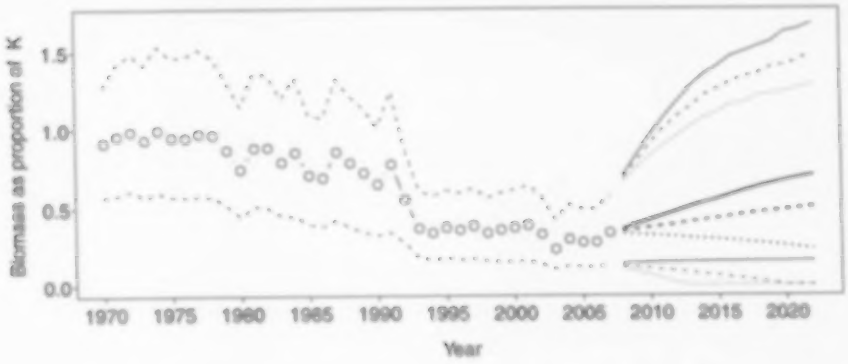
Fig. 7. Standardized residuals of predicted catch rates with the last 7 years of observation data removed. Filled circles (●) indicate years where observation data are present (1970 to 2000) and open circles (○) indicate that no observation data other than fishery removals are included (2000–2007). Panels *a*–*c* indicate the fishery independent trawl index, and *d*–*f* indicate the commercial longline catch rate index.



Biomass projections

Population projections using the derived parameter estimates from Model 3 suggest that the current landing limit of 750 t is sustainable and should result in a biomass increase (Fig. 8); however, robustness tests indicate a bias in predicted recovery rates, and the biomass predictions are

Fig. 8. Stochastic projections using Markov Chain Monte Carlo parameter realizations from the surplus production model that estimated a shape parameter for the trawl survey and assumed the longline index to be proportional to biomass (Model 3). Unbroken, dashed, and dotted lines are median and associated 95% credible limits of the biomass estimates corresponding to catch levels of 0, 750, and 1500 tons per year.



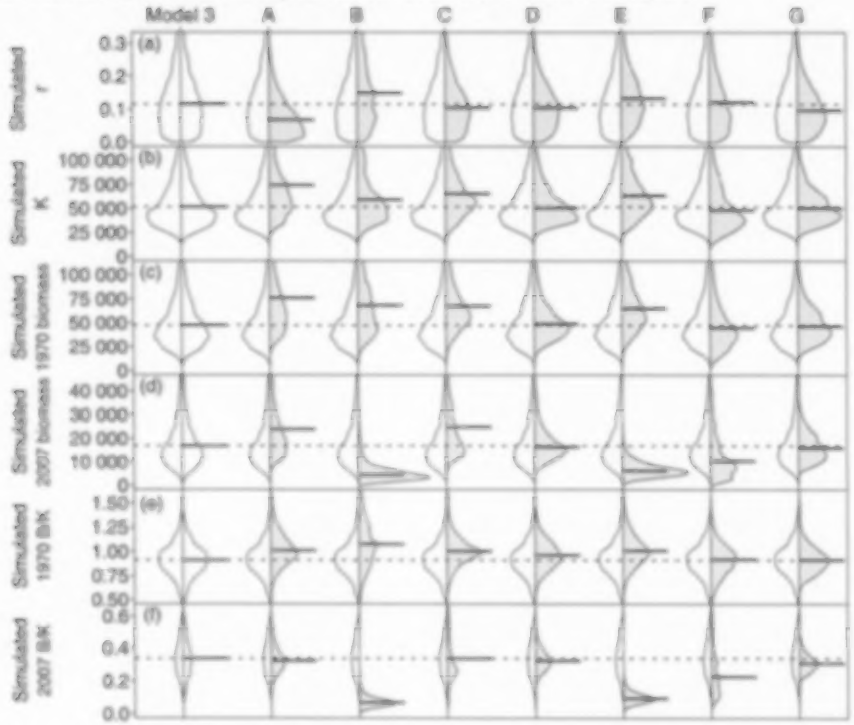
likely overly optimistic (Fig. 7). The projection predicts a median biomass increase to 50% of K by the end of the 15-year projection period, which equates to the biomass level that would give MSP under Shaefer model assumptions. In terms of risk, 4% of projected populations went extinct after 15 years at this landings limit. Terminal biomass estimates had wide credible limits, owing to the large uncertainty in the parameter values and stochastic nature of the projections. Indeed, some realizations of the joint posterior distribution for the r parameter were close to zero (3.7% were < 0.01) resulting in very little biomass production during the projection period. A landings limit of 1500 t was clearly unsustainable, with 30% of the simulated populations going extinct after 15 years. Reducing landings to zero resulted in predicted biomass increases to 70% of K after 15 years. An obvious limitation of the projections is that they are based on equilibrium conditions, which do not account for the age-structure of the population or recruitment time-lags. Furthermore, the robustness tests suggest that the models have poor predictive ability and tend to over predict biomass increases.

Simulations

Simulations provided a clearer picture of the benefits of including both indices and the consequences of model misspecification on parameter estimates. Beanplots comparing posteriors of the parameter estimates between Model 3 and the simulated data reveal that model misspecification can cause large biases in initial and terminal biomass estimates, and including both indices improved the precision of parameter estimates (Fig. 9). As with the models in the primary analysis, all models using simulated data had negative mean deviance, pD, and DIC.

The biomass trajectory derived from Model 3 is the basis for all the simulated data scenarios and is the baseline for comparison to all simulations (Table 2). Both posteriors in the Model 3 column are identical, and hence, the beanplots are symmetrical (Fig. 9; Model 3). The parameter estimates for Scenario A show that even when the model assumptions are consistent with the data, a single proportional index spanning the entire time-period (38 years) had insufficient power to fully recapture the parameters of interest (Fig. 9; scenario A). Scenario B describes the model fit that assumed proportionality to a single 38-year hyperdepleted index and had similarly diffuse posteriors for r, K, and B_0 as scenario A; however, the biomass estimate for 1970 was lower compared with both Model 3 and scenario A (Fig. 9; scenario B). A single proportional index spanning only the last 22 years (Fig. 9; scenario C), akin to only using the longline index and landings data, leads to similarly diffuse parameter estimates as those obtained by only using a single, longer, proportional time series (scenario A). However, the B/K ratios were less biased, compared with scenario A, although median estimates for K and biomass estimates were still biased high, compared with Model 3. This is likely a symptom of both the lack of CPUE data prior to 1986, and possible limitations of the Schaefer process model to fully capture the population dynamics. According to Schaefer model dynamics, the substantial landings prior to 1990 should have resulted in a decline in biomass during this period if the population was starting at carrying capacity. This was not observed in the simulated trawl survey data (which closely resembles the true trawl data; (Fig. 2)). Indeed, although some biomass decline was observed, the trawl survey declines only slightly, far less than should have been observed if the population was following Schaefer dynamics. The lack of observation data in the earlier years allows the model to fully follow Schaefer dynamics earlier in the time series, thus making K and initial biomass larger than what is estimated by the model that used both datasets. Using two indices that were proportional to biomass and modeled as such, allowed us to recapture the parameters of interest (Fig. 9; scenario D); both the posteriors and medians were almost identical to that of Model 3. The median of the posterior for r was slightly lower than the reference model (0.104 compared with 0.115), which is likely due to MCMC noise and (or) the observation error introduced to the simulated indices. In contrast, when the simulated trawl index is hyperdepleted and the shorter index is proportional to biomass, yet we do not account for nonproportionality in the model (scenario E), the posteriors of K and 1970 biomass were almost identical to those of Scenario B, which only used a simulated hyperdepleted trawl index, indicating that

Fig. 9. Select model parameters from simulation models. Beanplots (Kampstra 2008) compare the posteriors of select model parameters from Model 3 (white) to the posteriors from alternate model scenarios (grey posteriors in columns B to G), which use simulated indices of relative biomass derived from the median biomass trajectory estimated from Model 3. The broken horizontal lines are the median of posteriors of select model parameters from Model 3. The bold unbroken horizontal lines are the medians of the posteriors of the alternative model and data scenarios. Rows are estimates of the intrinsic rate of population increase, *r*, carrying capacity, *K*, biomass in 1970 and 2007, and the ratio of biomass divided by *K*. Model assumptions and data used are summarized in Table 2.



the trawl index is driving the estimates of these two parameters (Fig. 9, scenario E).

Scenario F had the same data characteristics as scenario E, but estimated a shape parameter for both indices. The model was able to obtain better parameters estimates by comparison with scenario E, with the exception of the 2007 biomass estimate, which was approximately 70% of the true value (Fig. 9, scenario F). The medians of the shape parameters were 0.81 (95% credible limits of 0.45–3.65) for the simulated proportional longline index, and 1.99 (95% credible limits of 1.13–8.93) for the simulated hyperdepleted trawl index both of which are very similar to those estimated by Model 2 in our primary analysis (Table 3). Finally, we were able to recapture the parameters of interest when the longer time-series was nonproportional and we included nonproportionality in the model (Fig. 9, scenario G). Similar to Scenario D, which correctly matched the model assumptions to the proportionality of the simulated data, the median of the posterior of r was slightly lower than the reference model. The model was able to estimate the nonproportional shape parameter close to its defined value of 2.5 (median $\beta = 2.44$).

Discussion

By using a Bayesian state-space modeling approach in WinBUGS, we were able to combine multiple indices in a single population model and identify and accommodate index nonproportionality, thereby improving estimates of cusk population trends and current status. There was weak evidence for nonproportionality of the commercial longline index; however, model fits substantially improved when a shape parameter was estimated in the observation equation of the trawl index, suggesting hyperdepletion of the trawl survey index for cusk. Using Model 3 as a baseline for the "true" biomass trajectory, we determined that including both indices in the model resulted in more precise and unbiased parameter estimates, and yielded better biomass estimates in the terminal and beginning years of the indices. COSEWIC's estimate of decline was primarily based on decline observed in the trawl survey index, and assumed that it was proportional to biomass. Our median estimates of decline of 59% between 1970 and 2001, and a 64% decline from 1970 to 2007, while still substantial, are much less severe than the 93% decline from 1970 to 2001 estimated in the COSEWIC assessment that used the raw index data (COSEWIC 2003). However, because our biomass estimates are smoothed by the model, and determining percent declines from raw index data can be unreliable, to make the estimates of decline of the two analyses more comparable we ran the model using only the survey data and estimated a median 89% decline from 1970 to 2001, assuming the

index was proportional to biomass. Use of the longline index alone, also leads to overestimates of cusk decline: a decline of 81% from 1970 to 2007, and 63% from 1986 to 2007 compared with 52% for this time period when both indices are used and nonproportionality of the survey index is included in the model (i.e., Model 3). Our lower estimate of decline will likely not have an impact on the COSEWIC designated status for cusk. Although the estimated decline is less severe, new aging analyses, although preliminary, suggest that generation time is approximately 15 years, rather than 9, as cited in the COSEWIC report (COSEWIC 2003). A decline of 64% in 2.5 generations is sufficient to warrant "threatened" status under the COSEWIC guidelines (COSEWIC 2009). Accounting for nonproportionality can substantially improve estimates of population trends; however, our simulations highlight that caution needs to be applied when using estimates of index nonproportionality from other analyses. For example, in Scenario F of our simulations, 70% of the probability density of the estimated shape parameter for the simulated longline index was less than 1.0 (median 0.81), even though the index was simulated to be directly proportional to biomass. This is an indication that there is confounding in the estimation of multiple shape parameters and thus using shape parameter estimates as informative priors in other analyses could lead to biased biomass trajectories. Furthermore, in our primary analysis, Model 4 had a median shape parameter estimate 0.41 and had more DIC support compared to Model 1 that assumed both indices were proportional to biomass. This estimate of hyperstability is far more severe than those estimated for directed commercial fisheries (Harley et al. 2001) and is therefore unlikely for a bycatch species such as cusk. Therefore, when specifying a model with shape parameter(s), it is important to consider whether there is an a priori reason to expect nonproportionality in the indices.

Our simulation models also show that including multiple indices substantially increases the power to recapture parameter estimates when nonproportionality is accounted for in the model when, and if, present in the data. We also discovered that DIC alone may not be a reliable metric for some Bayesian state-space model applications. An additional model we preliminarily tested, but is not described in the manuscript, was to test for a knife-edge change in catchability in the trawl survey in 1992 when the survey trawl index rapidly declined. According to DIC, this model had the most support using both the real and the simulated data, even though in the latter case we specified that a change in catchability was not responsible for the declines. This underscores the importance of using simulated data to investigate further the plausibility of the models.

We have shown that simply assuming the trawl survey index to be proportional to biomass can result in incorrect estimates of population change. This is of concern because this trawl survey is being used increasingly for population assessments of bycatch species, because it is frequently the only source of long-term fishery-independent time-series data on the east coast of Canada. Nonproportionality may be an issue for any species whose distribution is not well represented in the trawl survey design. While it maybe tempting to discard indices that have questionable proportionality relationships, in favor of other time-series data with known relationships to population biomass, this approach is unsatisfactory for a number of reasons. First, the index to biomass relationship is poorly known for most bycatch species and choosing one index over another will likely be ad hoc. Second, the potentially nonproportional index may be the longest time-series available and other indices may have little contrast and only begin after population declines have already occurred. Discarding long time-series has the potential to create shifting baselines (Pauly 1995) where current estimates of population status are viewed from a recent perspective. This can lead to underestimates of population decline (Rosenberg et al. 2005). Even with the inclusion of these relatively long time-series data, a lack of baseline data will still be a challenge because they began on the east coast of Canada in 1970, which is well after large scale industrial fishing began.

Although we were limited to using broad flat priors in this analysis, the Bayesian approach allows for ancillary information to be incorporated through the priors to reduce uncertainty in the parameter and biomass estimates and hence is particularly useful for data-poor species (Chaloupka and Balazs 2007; Swain et al. 2009). For example, demographic methods can be used to construct a prior for r (McAllister et al. 2001). We abandoned efforts to develop an informative r prior as the dearth of life history data and current uncertainty in aging would have resulted in a highly diffuse and bi-modal prior that would have added little to the analysis. Indeed, preliminary radio-carbon bomb calibration of cusk otoliths suggest that 95% of cusk are mature by 15 years and maximum age may be over 40 (P. Comeau, Marine Fish Division, Bedford Institute of Oceanography, Fisheries and Oceans Canada, Daertmouth, N.S., personal communication 2008), which is twice that of earlier estimates (COSEWIC 2003). Developing a credible prior for carrying capacity is also problematic as the true historical biomass of cusk before the onset of fishing will never be known with much precision. However, a joint posterior probability plot (not shown) of the r and K parameters indicate substantial confounding between the two. Although this can cause problems for parameter estimation, it also means an informative prior on r also provides information for the K parameter as well (McAllister et al. 2001).

The stochastic projections suggest that the current landing limit of 750 t should be sufficient to increase population biomass. However, the retrospective analysis we conducted by removing the last 7 years of data indicate that biomass should have increased over the last seven years but this has not been observed. This suggests that our projections have limited value for determining if biomass increases should be expected at the current landing limit and calls into question the utility of our parameter estimates for predicting population recovery. The lack of recovery may be due to a number of factors. First, landing limits may be ineffective because of high bycatch mortality. Although landing limits were designed to reduce fishery induced mortality, they may be ineffective because, as a relatively deep water species, cusk may suffer substantial barotrauma when captured. There are no estimates of bycatch mortality in the longline fishery, but estimates in the lobster fishery, which operates at similar depths, are >50% (DFO 2008). In our analyses, we equated landings with fishery removals and therefore we almost cer-

tainly underestimated true fishing mortality after 1999 when the first landings limit was implemented. Second, the Schaefer model does not include age-structure or recruitment time lags, and therefore our projections may exaggerate the predicted recovery rate. Evidence that time lags may be important can be seen in Fig. 2 where substantial biomass was removed in the early 1970s without a concurrent decline in the trawl survey index. Also, the symmetrical biomass production relationship of the Schaefer model may be unrealistic if age structure has a strong influence on the population production rate (Maunder 2003). Third, abnormally poor recruitment between 2000 and 2007 could also explain the lack of recovery. Alternatively, a regime change of reduced productivity or increased natural mortality in the latter period of the time series would result in a decrease population growth rate and be consistent with our poor model predictions. We attempted to model this by estimating separate r parameters before and after, the mid-1990s, but model fits did not improve, nor did the predictive ability of the model. Unfortunately, there are limited data to test these hypotheses.

In conclusion, our analysis suggests that the cusk fishery-independent trawl survey index suffers from hyperdepletion, which, if not accounted for, results in exaggerated estimates of population decline. The high levels of uncertainty in our parameter estimates are a result of the limited data available, as well as the low contrast and "one-way trip" trends in both catch rate indices. High levels of uncertainty in population parameters and historical biomass levels are characteristic of many bycatch species and management strategies that include these levels of uncertainty need to be employed. Managers also may seek to increase monitoring to achieve greater certainty in parameter estimates, and hence greater management control of this species. The effectiveness of the current landings limit to aid population recovery is uncertain as our robustness tests suggest that the population should be recovering, but monitoring data suggest that it is not. Further research is needed to estimate bycatch rates in the longline fishery to determine whether a landings limit is an effective management strategy for cusk recovery. In addition, further aging and age validation research is needed so that more realistic models, for example, that include time lags in recruitment can be used (e.g., Meyer and Millar 1999*a*; Millar and Meyer 2000). Although we were unable to include life-history information through the use of informative priors, the Bayesian approach is promising for the assessment of poorly monitored species where data is limited and time series have little information on population parameters.

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Life history strategy and impacts of environmental variability on early life stages of two marine fishes in the North Sea: an individual-based modelling approach

Ute Daewel, Myron A. Peck, and Corinna Schrum

Abstract: We employed a suite of coupled models to estimate the influence of environmental variability in the North Sea on early life stages of sprat (*Sprattus sprattus*), a small pelagic clupeid, and Atlantic cod (*Gadus morhua*), a demersal gadoid. Environmentally driven changes in bottom-up processes were projected to impact the survival and growth of eggs and larvae of these marine fish species in markedly different ways. We utilized a spatially explicit, individual-based model (IBM) to estimate larval fish survival and a 3D ecosystem model (ECOSMO) to provide variable prey fields. The model was applied to each of 3 years (1990, 1992, 1996) specifically characterized by interannual differences in water temperature in late winter and spring. Our results indicated that an important mechanism connecting environmental factors to larval fish survival was the match–mismatch dynamics of first-feeding larvae and their prey, which was species-specific because of (*i*) differences in the timing and locations of spawning, (*ii*) the duration of endogenously feeding life stages, and (*iii*) prey thresholds required for larval survival. Differences in transport processes also played an important role for the potential survival of larvae of both species.

Résumé : Nous employons une série de modèles couplés pour estimer l'influence de la variabilité environnementale dans la mer du Nord sur les premiers stades de vie du sprat (*Sprattus sprattus*), un petit clupéidé pélagique, et de la morue franche (*Gadus morhua*), un gadoïdé démersal. Nous avons prédit que les changements causés par l'environnement dans les processus ascendants devraient affecter la survie et la croissance des œufs et des larves de ces espèces marines de poissons de manière nettement différente. Nous utilisons un modèle basé sur l'individu (IBM) et spatialement explicite pour estimer la survie des larves de poissons et un modèle 3D de l'écosystème (ECOSMO) pour fournir des champs variables de proies. Nous avons utilisé cette modélisation avec les données de chacune de 3 années (1990, 1992, 1996) qui sont spécifiquement caractérisées par des différences interannuelles de température de l'eau à la fin de l'hiver et au printemps. Nos résultats indiquent qu'un important mécanisme qui relie les facteurs du milieu à la survie des larves de poissons est la dynamique d'appariement–mésappariement entre les larves lors de leur première alimentation et leurs proies; cette dynamique est spécifique à chaque espèce à cause (*i*) des différences dans le calendrier et la localisation de la fraie, (*ii*) de la durée des stades du cycle à alimentation endogène et (*iii*) des seuils de proies requis pour la survie des larves. Des différences dans les processus de transport jouent aussi un rôle important dans la survie potentielle des larves des deux espèces.

[Traduit par la Rédaction]

Introduction

The North Sea (Fig. 1) is a highly dynamic shelf sea system in terms of both physical and biological processes. The main cyclonic circulation pattern that comprises transport processes at the open boundaries as well as residual currents (e.g., wind, tides, and baroclinic currents) is superimposed by smaller scale dynamics with high frequencies that are ecologically highly relevant. For example, strong tides and river runoff interact with bottom topography to produce a complex hydrographical situation including frontal zones separating well-mixed, shallow, near-coastal regions from deeper, seasonally stratified areas in the southern North Sea (e.g., Otto et al. 1990; Schrum 1997). These frontal zones can be extremely productive areas supporting a high biodiversity of marine fauna, including relatively dense aggrega-

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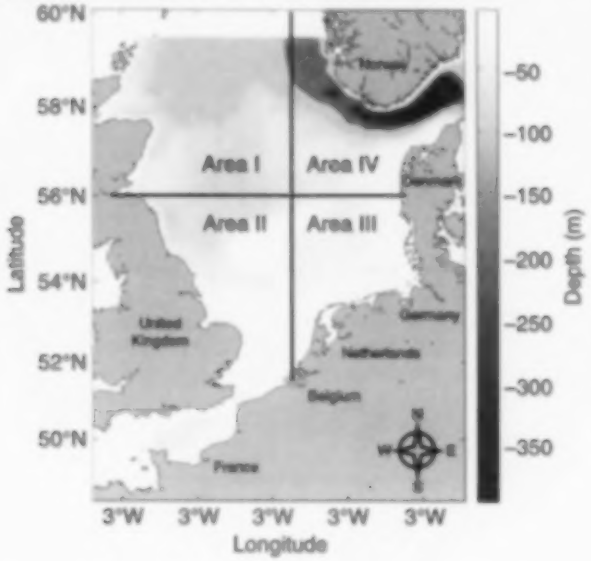


Fig. 1. North Sea model domain and topography and the locations of the four North Sea subareas (partitioned at 4°E and 56°N) employed in the analyses of 3D model results.

tions of larval fish, their prey, and their predators (e.g., Kiørboe et al. 1988; Munk et al. 1999). Both physical and biological features of the North Sea (and other shelf seas) are directly impacted by changes in atmospheric forcing (e.g., air temperature, wind velocity), and the link between environmental variability and productivity in North Sea fish fauna has been discussed for the last century (Hjort 1914). Given the pronounced seasonality in physical and biological factors, species that spawn at different times of the year in the North Sea have likely adopted different life history strategies that may make them either more or less vulnerable to environmental changes. The fact that some fishes exist at their latitudinal extreme in the North Sea is a second feature that makes the composition of the fish assemblage dynamic with respect to environmental changes (Beare et al. 2004; Alheit et al. 2005).

Sprat (*Sprattus sprattus*) and Atlantic cod (*Gadus morhua*) are two important members of the North Sea fish community that have different life history strategies and different trophodynamic roles. Sprat is a small, pelagic "wasp-waist" species (e.g., Cury et al. 2000), important to both "top-down" and "bottom-up" processes (e.g., Köster and Möllmann 2000), whereas Atlantic cod is a demersal gadoid that has traditionally been one of the most abundant predatory fish in the North Sea. The North Sea forms the southern limit of the distribution of Atlantic cod (Planque and Frédou 1999) and the northern limit of the distribution of sprat, and this is reflected in the difference in life cycle scheduling observed for these species. North Sea cod spawns in winter and spring (January–May, peak February and March; Rogers et al. 2001), while the warmer-water sprat spawns in the spring and summer (April–August, peak in May and June; Munk 1993). Both of these species produce pelagic eggs that hatch into pelagic larvae and, owing to the different spawning times, early life stages of these species experience markedly different North Sea environments (e.g., temperatures, prey fields).

During the last 30 years, spawning stock biomass of sprat has been stable or increasing while that for Atlantic cod has markedly declined in the North Sea (Heath 2005; International Council for the Exploration of the Sea 2005). Unfortunately, explaining these patterns is difficult, since both species are commercially exploited and disentangling the influence of multiple drivers (such as climate and fishing pressure) remains problematic. In North Sea cod, a clear relationship between cold mean water temperatures and high levels of cod recruitment has been reported by several investigators (e.g., Planque and Frédou 1999; Brander and Mohn 2004), but the impact of water temperature appears strongest at low levels of cod spawning stock biomass (O'Brien et al. 2000). Causal mechanisms (e.g., predator–prey match–mismatch dynamics) behind these temporal trends have been inferred from correlations between climate-driven changes in both the size and species composition of calanoid copepods in the North Sea and changes in cod recruitment strength (Beaugrand et al. 2003). Clearly, one can assume that changes in both water temperature and prey availability can impact the recruitment of North Sea cod (and other marine fish species in other regions), and these statistical (correlative) studies are an extremely important first step towards understanding which physical and biological processes may be important regulators of marine fish recruitment.

Many recruitment hypotheses suggest that rates of survival and growth are linked during the early life of marine fish (Houde 2002) and that small changes in these rates can cause large differences in recruitment (e.g., Houde 1989; Campana 1996) because of the interaction between body size and the risk of mortality in marine food webs (Shin and Cury 2004; Pope et al. 2006). A number of biophysical individual-based models (IBMs) have been employed to examine how different environmental factors influence growth and survival of early life stages of a variety of species, including Atlantic cod (Fiksen and MacKenzie 2002; Lough et al. 2005) and sprat (Kühn et al. 2008; Peck and Daewel 2007). These mechanistic IBMs include species-specific physiological attributes and can provide estimates of environmental requirements (e.g., temperature–prey combinations) for larval survival. A recent advancement has been to couple a three-dimensional (3D) biophysical IBM to a 3D NPZD (nutrient, phytoplankton, zooplankton, detritus) ecosystem model (Daewel et al. 2008*a*, 2008*b*) to include spatially explicit changes in key abiotic (hydrographic environment) and biotic (prey fields) factors. Daewel et al. (2008*a*) utilized this coupled modelling approach to investigate the spatial variability in survival, growth, and aggregation of sprat larvae on a seasonal time scale in the North Sea. They identified spatial and temporal differences in growth rates (driven by differences in temperature and prey fields) and suggested that these differences were the likely mechanism responsible for the accumulation of larval fish at frontal areas in the southern North Sea (Daewel et al. 2008*a*).

The objective of the current modelling study was to illustrate how interannual, atmospherically driven bottom-up changes in key abiotic and biotic factors could influence the

survival of early life stages of two species having somewhat different life history strategies (e.g., spawning season, larval energetics). We employed the coupled model system in each of 3 years (1990, 1992, and 1996) that differed with respect to North Sea winter–spring water temperature to investigate spatial–temporal differences in rates of survival and growth in early life stages of both Atlantic cod and sprat. Our modelling study was designed to identify causal factors and key processes that help explain recent trends in North Sea populations of cod and sprat. On a more generic level, we wanted to explore how interspecific differences in life history might mediate the effects of environmentally driven changes in bottom-up factors on growth and survival of marine fish early life stages.

Materials and methods

Model description

A coupled model system (hydrodynamic model, NPZD model, fish early life stage IBM) previously described by Daewel et al. (2008*a*) was utilized to assess the impact of both abiotic and biotic factors on the transport, growth, and survival of eggs and larvae of sprat and cod. An IBM was used to depict the development, growth, and potential survival of fish early life stages (eggs and larvae) as well as advective and diffusive transport (Lagrangian approach). The IBM was coupled online to a hydrodynamic model (Schrum and Backhaus 1999). Finally, prey fields required for simulating the foraging, growth, and survival of larval fish were derived from the 3D output of a biophysical ecosystem model "ECOSMO" (Schrum et al. 2006*a*). The IBM was coupled to the 3D hydrodynamic model using a 20 min time step, which allowed the impacts of tidal dynamics as well as the diurnal changes in short-wave radiation to be resolved, an important prerequisite for adequately depicting the transport and foraging by larval fish.

Coupled hydrodynamic–NPZD model ECOSMO

Detailed descriptions were previously published regarding the 3D hydrodynamic core (that provided temperature, turbulence, and transport) by Schrum and Backhaus (1999) and the NPZD module (from which prey fields were obtained) by Schrum et al. (2006*a*). The model equations were solved on a staggered Arakawa-C-grid for the North Sea and Baltic Sea with a horizontal resolution of 6 nm (1 nm = 1852 m). To resolve stratification, a 5 m vertical grid was used in the upper 40 m. Besides atmospheric boundary conditions at the surface (provided by NOAA National Centers for Environmental Prediction (NCEP)–National Center for Atmospheric Research (NCAR) reanalysis data; Kalnay et al. 1996), monthly means of land-based freshwater runoff and nutrient loads were required to run the model, and details on data sources were given by Schrum and Backhaus (1999). At the open boundaries to the North Atlantic and the English Channel, changes in sea surface elevation were prescribed to introduce tidal dynamics via the dominant, partial M_2, S_2, and O_1 components. The model provides realistic estimates of the hydrodynamics of the North Sea and Baltic Sea and its spatial and temporal variability on time scales of days to years as was shown by Janssen (2002).

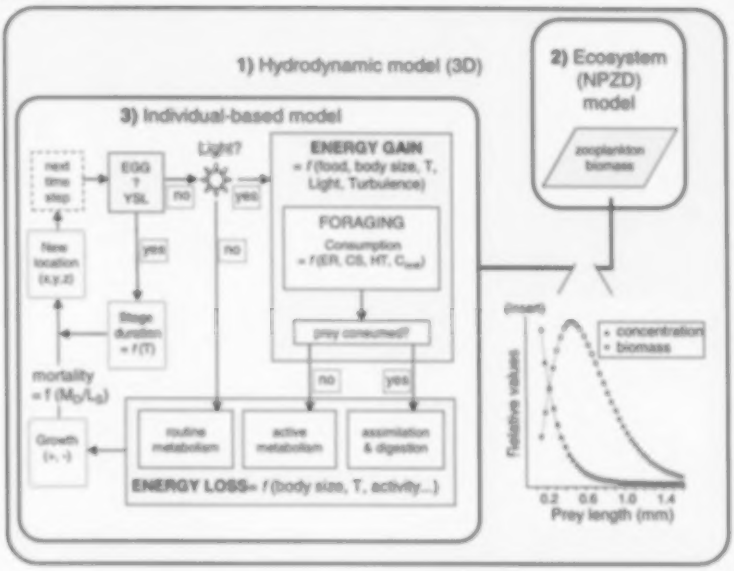
The ecosystem (NPZD) model was developed, tested, and validated by Schrum et al. (2006*a*, 2006*b*). This model has 12 state variables and was developed to simulate different macronutrient limitation processes that are particularly important to lower trophic level dynamics in the North Sea (Schrum et al. 2006*a*). For this purpose, it included three nutrient cycles (nitrogen, phosphorus, and silicon), two phytoplankton functional groups (diatoms and flagellates), and two zooplankton groups (herbivores and omnivores). Climatic boundary and initial conditions for the NPZD model were prescribed for nutrients, temperature, and salinity. Details about data sources are provided by Schrum et al. (2006*a*). Schrum et al. (2006*a*) published results from 1-year model integrations for few selected years, with initial condition of winter plankton concentrations obtained from World Ocean Atlas 2001 (WOA2001, Conkright et al. 2002). Neither the WOA2001 nor any other sources provide coherent and adequate estimates for climatic zooplankton biomass data for the North Sea. In our climatic simulations, we therefore related the initial zooplankton carbon biomass to the climatic winter phytoplankton concentration, with the zooplankton biomass chosen to be 20% of the climatic winter phytoplankton biomass. As shown in the model validation performed by Schrum et al. (2006*a*), our initial condition underestimated the observed zooplankton winter biomass. Moreover it does not allow for good representation of interannual variability in winter zooplankton estimates, since the 1-year runs always started from the same climatic conditions. For the study presented here, therefore, we used the zooplankton data from a 24-year (1980–2004) continuous model integration (S. Svendsen, University of Bergen, Geophysical Institute, N-5007 Bergen, Norway, unpublished data), starting from the initial conditions as described in Schrum et al. (2006*a*). This simulation improved the modelled levels of winter (February to mid-March) zooplankton (~3 mg C·m^{-3}) compared with the climatic 1-year simulation (~0.1 mg C·m^{-3}). Similarly to Schrum et al. (2006*a*), we assessed the zooplankton biomass against winter average values from in situ experiments. For example, the SAHFOS continuous plankton recorder (CPR) scaled biomass estimates were 1.0–4.0 mg C·m^{-3} and <1.0 mg C·m^{-3} for carnivorous and omnivorous zooplankton, respectively, in the majority of the North Sea (Broekhuizen et al. 1995). Furthermore, measurements performed between February and March 1987 during the "ZISCH" project (German Federal Ministry of Education and Research, BMBF) reported a North Sea-wide mean zooplankton biomass of 7.0 mg C·m^{-3} for the respective time period (Krause and Knickmeyer 1992; Krause et al. 1995).

The NPZD model was coupled offline to the spatially explicit IBM using methods described by Daewel et al. (2008*b*), which converted estimates of bulk zooplankton biomass (mg C·m^{-3}) into a prey size spectrum (using specific size bins) required for foraging by larval fish. The conversion is based on the assumption that the size spectrum of zooplankton in the North Sea follows an exponential decrease in abundance with increasing zooplankton size (Fig. 2, insert).

Individual-based model

The IBM was structured as an *i*-state configuration model,

Fig. 2. Conceptual diagram of the coupled model structure. The IBM is implemented in the hydrodynamic core. The IBM consists of the egg, yolk-sac larval, and feeding larval stages (EGG, egg stage; YSL, yolk sac larvae; L_S, larval length; M_D, larval dry mass; T, temperature; ER, encounter rate; CS, capture success; HT, handling time) and a Lagrangian transport module. The ecosystem model "ECOSMO" (Schrum et al. 2006*a*) provides zooplankton biomass that is converted into a size-specific prey field (Insert) and utilized in the IBM foraging subroutine according to Daewel et al. (2008*b*).



treating individuals as explicit entities (Caswell and John 1992). The development of endogenously feeding life stages (eggs and yolk-sac larvae) was parameterized based on empirical (laboratory-derived) relationships. The formulation for exogenous feeding larvae was more complex and based on a balanced bioenergetics approach that accounted for energy gain (ingestion: represented by food consumption C and assimilation efficiency β) and energy loss due to metabolism (R) and specific dynamic action (SDA) (Fig. 2):

$$G = C\beta(1 - \mathrm{SDA}) - R \quad (1)$$

The IBM parameterizations were species-specific and based on previously published models for both sprat (Daewel et al. 2008*a*) and Atlantic cod (Lough et al. 2005), while the latter needed to be slightly modified for use in our coupled model system. In the following section, we provide a general description of the IBM and the major differences between the formulations for Atlantic cod and sprat, while details about the model parameterization and its implementation for both species are given in Appendix A.

IBM: nonfeeding stages

The development of eggs and yolk-sac larvae was based upon previously published functions estimating the time to hatch for eggs and the time required for 95% yolk absorption in yolk-sac larvae at different temperatures. These functions were available for Atlantic cod (Jordaan and Kling 2003; Geffen et al. 2006) and sprat (Thompson et al. 1981; Alshuth 1988). Based upon these functions, the duration of the endogenous feeding period was longer in sprat compared with cod at the same (constant) temperature. However, eggs and yolk-sac larvae of cod can survive and develop at colder water temperatures than those of sprat (see Fig. 3*a*).

IBM: food consumption

In exogenously feeding larvae, foraging and growth were depicted using subroutines that had the same structure for both cod and sprat but with species-specific parameter estimates. The mass of total prey consumed was calculated according to Letcher et al. (1996) as a function of encounter rate ($N_{L_S,i}$), capture success ($\mathrm{CS}_{L_S,i}$), and handling time ($\mathrm{HT}_{L_S,i}$)

$$C = \frac{\sum_i m_i \times N_{L_S,i} \times \mathrm{CS}_{L_S,i}}{1 + \sum_i N_{L_S,i} \times \mathrm{HT}_{L_S,i}} \times \Delta t \quad (2)$$

where i represents the index of a certain prey type with a specific prey length (pl_i) and prey mass (m_i). Larval sprat and cod were not expected to feed on all prey sizes available, but select from encountered prey using an optimal foraging approach (Letcher et al. 1996). Specifically, the different prey types were ranked according to three factors (m_i, $\mathrm{CS}_{L_S,i}$, $\mathrm{HT}_{L_S,i}$) and sequentially included in the diet on the basis of rank until the profitability decreased. The maximum prey size that a larva with a certain length is able to ingest is determined by its mouth gape opening, which is markedly different in early life stages of cod and sprat. Formulations of the maximum prey size versus larval size were based upon measurements made of the prey in gut contents of sprat (Voss et al. 2003; Dickmann et al. 2007) and Atlantic cod (G. Lough, Northeast Fisheries Science Center, Na-

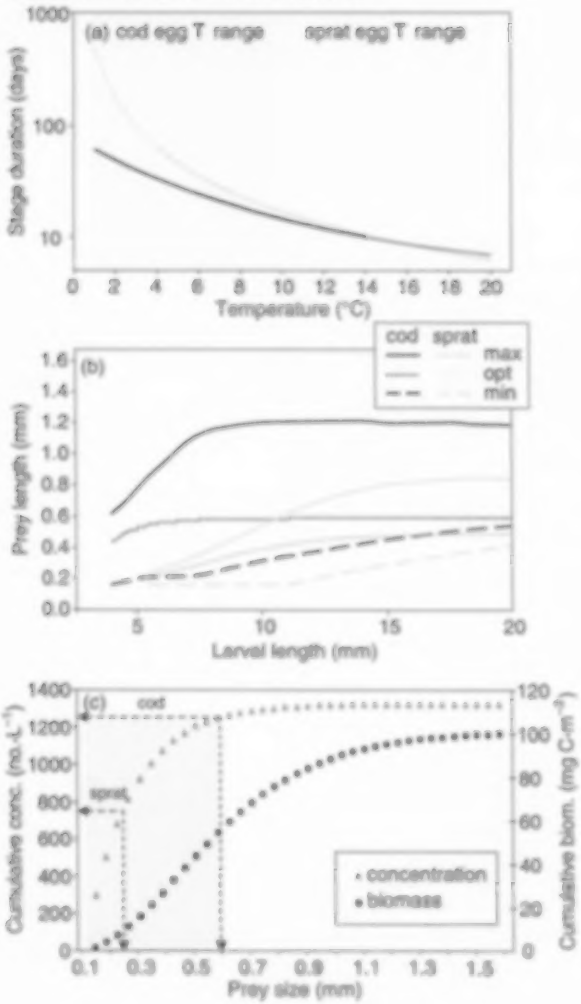


Fig. 3. IBM estimates based upon simple, species-specific parameterizations, including (*a*) cumulative duration of the egg and yolk-sac stages: the dashed line denotes ranges in temperatures (*T*) causing increased egg mortality based upon published laboratory data; the shaded area in the background indicates the potential range of temperatures likely experienced by eggs and yolk-sac larvae in the North Sea. (*b*) Prey size (length, mm) consumed by Atlantic cod and sprat versus larval fish standard length (mm). All prey sizes between minimum (dashed line) and maximum (solid line) were included in the modelled larval diet. Dotted lines indicate optimal prey sizes calculated by the model. (*c*) Cumulative prey abundance (open triangles) and biomass (solid squares) versus prey size class and the prey size classes utilized by first-feeding cod and sprat larvae (grey shaded areas). Cumulative prey size and biomass distributions were based upon a total zooplankton biomass of 100 mg C·m^{-3} that was separated into 40 μm size classes using methods outlined by Daewel et al. (2008*b*).

tional Marine Fisheries Service, Woods Hole, MA 02543, USA, unpublished data). A comparison between the species indicated that cod was able to profitably feed on larger prey items and on a larger prey size spectrum compared with similar-sized sprat larvae (Fig. 3*b*). Young (first-feeding) larval sprat are able to ingest relatively small prey items (prey size < 250 μm) compared with first-feeding cod (prey size < 600 μm). The fraction of the total prey biomass (range in prey lengths between 150 and 1600 μm) available to first-feeding sprat was predicted to be quite small (10%) compared with that available to cod (50%) (Fig. 3*c*).

One difference between the model formulations for cod and sprat was the parameterization for $N_{L_0,i}$ that depends on the reactive distance (RD_i) and the velocity component of encounter rates (V). Here, sprat was considered to be a cruise predator (see Daewel et al. 2008*a* for details), while cod larvae were considered pause–travel predators, searching for prey during pauses between swimming events (Lough et al. 2005).

The daily food consumption (C_{day}) was restricted to an upper limit ($C_{day} = \min(\sum_{day} C, C_{max})$), representing a satiation effect incorporated into the model to prevent overfeeding (e.g., Letcher et al. 1996). Maximum consumption (C_{max}) in sprat was based on an empirically derived formulation (for details see Daewel et al. 2008*a*), while a mechanistic approach was taken to prevent overfeeding by cod. Here, the maximum gut content (GC_{max}) and gut evacuation rate (GER) determined the space available in the gut and hence the amount of prey that could be ingested by a larva during any model time step.

IBM: metabolic losses

Consumed prey mass was reduced by an assimilation efficiency (β), specific dynamic action (SDA_m), and other metabolic losses. The latter included components accounting for standard (R_S) and active (R_A) rates of energy loss. Metabolic losses due to activity occurred during the day and were approximated by increasing standard metabolism by a factor (k) to account for activity.

IBM: length growth and mortality

For exogenously feeding sprat and cod larvae and postlarvae (7.0–40.0 mm L_S), allometric relationships between dry mass and standard length were available (Peck et al. 2005). Potential larval survival (PLS) was included in both the cod and sprat IBMs. In cod, PLS was equal to the percentage of larvae remaining above a critical minimum mass (M_{min}) at age (t). Larvae that lost mass and were $<M_{min}$ were considered to have died from starvation and were removed from the simulation. For sprat, partitioning between growth in mass and length depended upon larval condition factor (ϕ) (mass-at-length). If growth in dry mass was positive and $\phi \geq 1$, the larva increased its standard length. If growth in dry mass was continually negative and ϕ was <0.4, the larva died. Mortality due to predation was not included in this study.

0D model runs: experimental setup

To compare the performance of the IBM for exogenously feeding larvae of Atlantic cod and sprat, 0D model runs were performed. Here the IBM was not coupled to the hydrodynamic or ecosystem models, but environmental conditions (e.g., temperature, prey biomass, light, turbulence level) were predefined and kept constant during each simu-

lation. Two numerical experiments were conducted to assess the impacts of temperature and prey availability on simulated growth and survival. In experiment 1, larval growth rate in length (mm·day^{-1}) was calculated under ad libitum feeding conditions (150 mg C·m^{-3}) at two different temperatures. The second 0D experiment examined the interrelationship between temperature and prey requirements by performing simulations at five different constant temperatures (4, 8, 12,16, 20 °C) and at different levels of prey biomass ranging from 10 to 250 mg C·m^{-3} for sprat and from 5 to 100 mg C·m^{-3} for cod. At each temperature, the prey biomass level at zero growth rate was iteratively determined. The simulations were stopped when the larvae reached a length of 10 mm, and the mean growth rate in length for the whole simulation period was calculated. In both 0D experiments, light intensity was set to be sufficient for feeding, and photoperiod was maintained at 14 h.

Note that these 0D simulations were conducted under relatively low levels of turbulence (10^{-6} W·kg^{-1}). The maximum turbulent dissipation rates encountered by larvae in the North Sea can be >10^{-6} W·kg^{-1} (e.g., Simpson et al. 1996), constituting environmental conditions where larval survival would only be possible at higher levels of prey biomass. A sensitivity study previously conducted on the sprat IBM indicated a dome-shaped relationship between growth and turbulence and that larvae feeding was poor at high turbulent dissipation rates (Daewel et al. 2008*a*). However, the analysis also indicated that larvae did not die of starvation at high turbulence levels if prey biomass levels were high.

3D model runs: experimental setup

In 3D-coupled model simulations, particles representing cohorts of eggs that could develop into larvae were released each day during the North Sea spawning period for cod (1 January to 30 April) and sprat (1 April to 31 July). A total of 72 506 cohorts was released each day in a homogeneous distribution (horizontal 6 nm × 6 nm grid, vertical every 5 m) across the entire North Sea (see Daewel et al. 2008*a*, their figure 1*b*). Although sprat and cod do not spawn throughout the entire North Sea, utilizing a homogeneous distribution of release areas provided spatial estimates of habitats that supported potential larval survival (PLS) independent of previously observed (realized) spawning grounds. An estimate of PLS was obtained for each horizontal grid point from the average percentage of surviving cohorts that were released at all depths on each day within that grid box throughout the entire spawning season of cod (January–April) and sprat (April–July). We then could compare the spatial estimates of PLS to the locations of known spawning grounds to help verify the model approach. We also calculated the duration of endogenously feeding stages and the position of each cohort prior to first feeding with respect to spawning time and location to identify the role of transport patterns in terms of predator (larvae) – prey (zooplankton) overlap. An estimate of the potential magnitude of match–mismatch was obtained by comparing the seasonal variability of mean zooplankton biomass in each subarea to depth-averaged larval concentrations (the sum of all larvae from first-feeding to 20 mm L_S within each horizontal grid box divided by the total depth (m) at the horizontal position) for each day of a simulation.

We chose to compare 3D simulation results of PLS, transport, and match–mismatch among 3 years (1990, 1992, and 1996) that display different mean (North Sea-wide) winter water temperatures. The years 1990, 1992, and 1996 represented a relatively warm winter, an average winter ($\Delta T_{1992-1990}$ ~ –0.6 °C), and an extremely cold winter ($\Delta T_{1996-1990}$ ~ –1.7 °C), respectively. As a justification for basing our choice on winter temperatures, the largest interannual variability in simulated water temperatures (Fig. 4) exists in the North Sea during the coldest period of the year (February and March) (Janssen 2002), which coincides with the main spawning period for Atlantic cod in this region. An empirical orthogonal function (EOF) analysis conducted on spatiotemporal variability in water temperature (Janssen 2002) and modelled zooplankton biomass (Schrum et al. 2006*b*, their figure 8) indicated that the prevailing patterns were strongly correlated with the North Sea hydrography. For example, the largest seasonal temperature differences and variability in zooplankton biomass were estimated for shallow, tidally well-mixed areas along the coast, particularly in the southern North Sea, while the central and northern portions of the North Sea exhibited less temperature variability, are seasonally stratified, and are less productive. To simplify the interpretation of our 3D model results (as well as provide spatially explicit analyses of the results), we separated the North Sea into four different areas (see Fig. 1) based upon regional differences in prey and temperature predicted by the coupled hydrodynamic and NPZD models.

Results

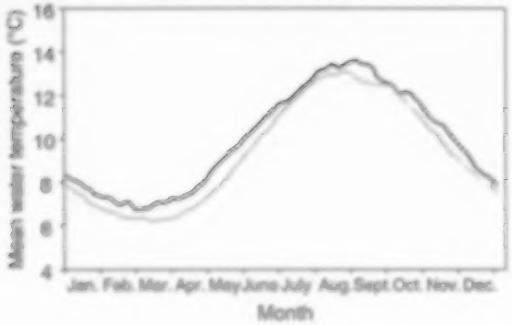
0D model simulations

Despite differences in the formulations and parameterizations of the cod and sprat foraging and growth IBM subroutines, the results of 0D model simulations indicated that temperature-specific growth rates of cod and sprat larvae <20 mm L_S were quite similar when larvae were not food-limited (Fig. 5*a*). However, more prey was required for maximum growth at any temperature in sprat (~30–200 mg C·m^{-3}) compared with cod (~7–50 mg C·m^{-3}), and model growth rates of cod and sprat were markedly different when food was limiting (Fig. 5*b*). Although the zooplankton biomass (concentration) required for survival increased with increasing temperature in both species (owing to temperature-dependent metabolic costs), interspecific requirements were markedly different. The results indicated that the critical amount of prey required to support the survival of first-feeding larval sprat was about fivefold higher than that for larval cod (Fig. 5*b*).

3D results: potential larval survival

When sprat and cod eggs were released homogeneously in the North Sea, not all areas supported PLS. Based upon spawning location and spatial variability in mean PLS, suitable spawning grounds for both sprat and cod were restricted to the southern North Sea (Fig. 6). The highest mean PLS resulted from spawning in nearshore areas of the Dutch and German coasts and in the vicinity of Dogger Bank. Although the location of suitable spawning grounds estimated for sprat (Figs. 6*d*–6*f*) appeared to be similar in each of the 3 years, this was not the case for Atlantic cod

Fig. 4. North Sea mean water temperature in 1990 (black line), 1992 (dark grey line), and 1996 (light grey line) as estimated by the hydrodynamic model employed in this study.



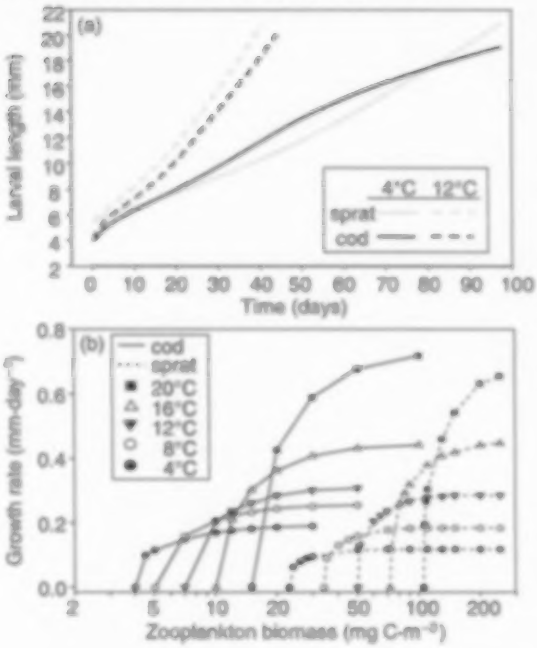
(Figs. 6*a*–6*c*), where the spatial extent and magnitude of areas supporting PLS varied among the years.

Our results also predicted an interannual trend as well as differences among the four North Sea regions in PLS. Among the years, cod PLS decreased with increasing average winter water temperature (January–April) (Fig. 7*a*), a trend that was consistent within each of the four subareas. However, at the same average winter water temperature, PLS was always two to four time higher for spawning (particle releases) in the southern areas (Areas II and III) compared with northern areas (Areas I and IV) of the North Sea. For sprat, PLS was also greatest in southern areas but was unrelated to interannual changes in the average water temperature (April–July) (Fig. 7*b*). Intraannual differences in monthly mean PLS were also evident, with largest differences for cod during the earliest spawning months (January–February: relative low PLS) compared with later spawning months (March–April: relative high PLS) (Fig. 7, Insert 1). Specifically, cod PLS during the coldest year (1996) was higher compared with the warmer years. In contrast, interannual differences in sprat PLS were much smaller when compared with cod. Furthermore, PLS in sprat was generally higher in earlier spawning months (April–May) compared with later spawning months (June–July) (Fig. 7, Insert 2).

3D results: transport

Despite the difference in spawning time, the general transport pattern for cod and sprat cohorts prior to first feeding was similar in each of the four potential spawning regions (Areas I–IV; Fig. 8). Generally, stronger transport was projected for cod cohorts compared with sprat in all areas except within Area I, where larvae were strongly transported into the northern and central North Sea (Fig. 8*a*). From the German Bight (Area III, Fig. 8*c*), there was a strong northward transport of early life stages of both species and a low percentage of westward transport into the Southern Bight (Area II). Similar percentages of cohort released in the Southern Bight drifted into Areas I and III (Fig. 8*b*). Some larval cohorts were lost from the model domain. For example, up to 5% of larval sprat or cod cohorts were transported northward out of Area IV (Fig. 8*d*) before they started exogenously feeding. This transport is caused by the Norwegian coastal current and appears to be more important for the spring- and summer-spawned sprat individuals. On the other hand, a greater part of cod cohorts were exposed to a westward transport pattern.

Fig. 5. IBM, 0D simulation results for sprat and Atlantic cod. (*a*) Larval standard length (L_S) vs. time at 4 and 12 °C under ad libitum feeding conditions (prey biomass = 150 mg C·m^{-3}). (*b*) Growth rates for <10 mm L_S sprat and Atlantic cod larvae versus total zooplankton (prey) biomass at each of five different temperatures. Note that the prey spectrum that first-feeding larvae are able to utilize is not the same for sprat and Atlantic cod.

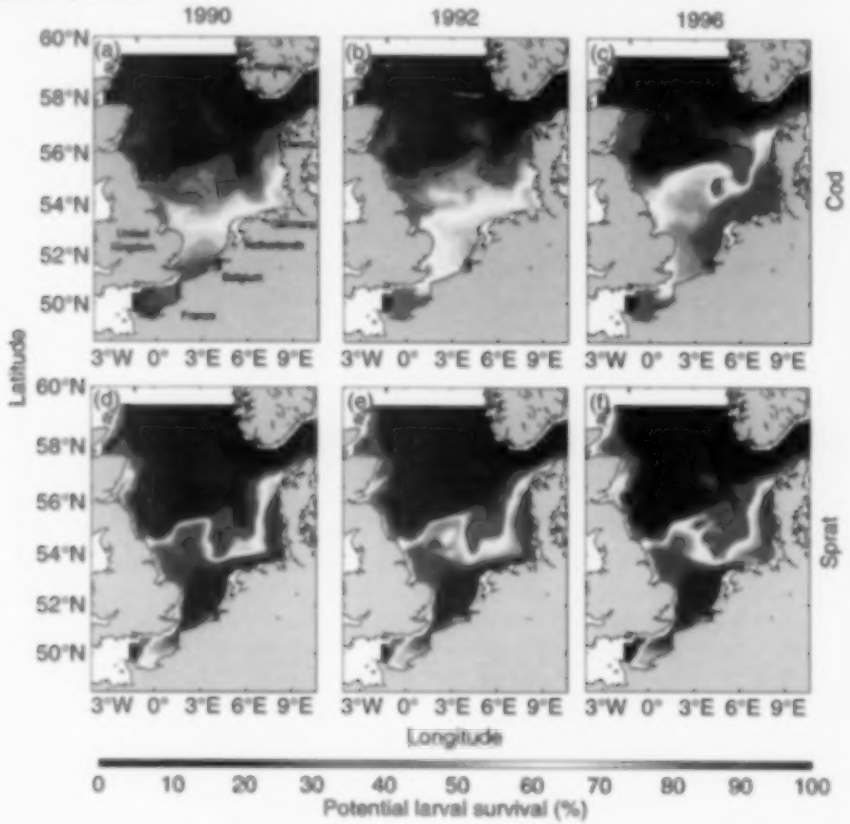


The results indicated stronger transport of eggs and yolk-sac larvae for cod spawned in 1990 and 1992 compared with sprat (Figs. 8*a*–8*d*). Moreover, the transport of cod exhibits a more pronounced interannual variability than that of sprat (Figs. 8*a*–8*d*). This was particularly evident in 1996, an exceptionally cold year that exhibited a markedly different transport pattern compared with either 1990 or 1992. Despite the very cold temperatures (and hence slow rates of development and longer durations of endogenous feeding periods for cod compared with sprat), transport out of the southern areas (Areas II and III) was lower for cod compared with sprat in that year. Moreover, the number of individuals leaving Areas II and III in a northward direction was much lower in 1996 (~4.4 times greater in 1990), and the dominant direction of transport of individuals spawned in the German Bight (Area III) was in a westward direction, following a weak anticyclonic circulation pattern.

3D results: match–mismatch dynamics

A comparison of monthly mean values of larval cod and sprat concentration and zooplankton biomass in each subarea revealed the potential for larvae to match with favourable feeding conditions (Fig. 9). In general, the modelled seasonal zooplankton dynamics indicated a slightly later onset of the zooplankton production in the western parts of the

Fig. 6. Model estimates of spawning grounds supporting potential survival of larval Atlantic cod (*a*–*c*) and larval sprat (*d*–*f*) for 1990, 1992, and 1996. Estimated potential survival was the mean value calculated for the whole spawning period (Atlantic cod: January–April; sprat: April–July) at each spawning location.



North Sea in Area I (Fig. 9*c*) and Area II (Fig. 9*f*) compared with the eastern regions in Areas III and IV (Figs. 9*i* and 9*l*). Furthermore, the spring peak in biomass (February–March) was accompanied by higher maximum values in the east, with highest zooplankton biomass obtained in 1990 and 1992 compared with 1996.

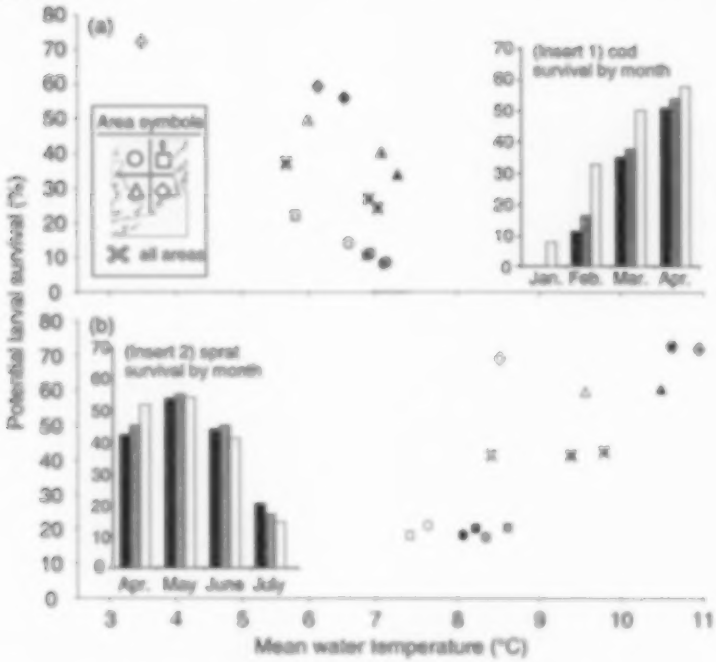
The seasonality in the concentration of feeding larvae was markedly different in Atlantic cod and sprat, particularly in relation to temporal changes in zooplankton biomass. While the occurrence of larval sprat (Figs. 9*b*, 9*e*, 9*h*, 9*k*) overlapped (matched) the timing of maximum prey biomass, the maximum occurrence of cod larvae (Figs. 9*a*, 9*d*, 9*g*, 9*j*) appeared earlier in the season and suggested mismatch situations with prey early in the year (January–March). Specifically during the warmer years (1992, 1993), our results suggest lower larval concentrations in months with relatively high prey biomass (March–July) compared with the colder year 1996 (Figs. 9*a*, 9*d*, 9*g*, 9*j*). In contrast, sprat larvae experienced favourable feeding situations (a match with zooplankton biomass) in all 3 years. However, simulations also predicted marked interannual variability in the seasonality of sprat larval concentration. The first increase in sprat larval concentration occurred in May, where higher concentrations were predicted during the warmest year (1992) in each area (Figs. 9*b*, 9*e*, 9*h*, 9*k*). In contrast, the concentration of sprat larvae was higher somewhat later in the year during 1996.

Discussion

Observed vs. predicted spawning sites

The model simulations for Atlantic cod and sprat identified potential spawning grounds (PSG, based upon larval survival) mainly in the southern part of the North Sea that coincided with areas observed (e.g., Pitois and Fox 2006) and predicted by our NPZD model to have maximum amounts of secondary production and zooplankton biomass. For both sprat and Atlantic cod, coarse maps of spawning activity were published by Rogers et al. (2001, their figures 3.2.2.1 and 3.2.13.1, respectively), and more detailed maps of North Sea cod spawning activity were published by Fox et al. (2008). Spawning by sprat takes place over broad areas of the southern North Sea and along the English coast (Rogers et al. 2001), a spatial pattern that agrees well with our model-based estimates of sprat PSG. For Atlantic cod, the spatial extent of peak spawning activity also agreed with our PSG. However, over a broad area, spawning appears to be restricted to a number of smaller "pockets", including areas associated with Dogger Bank, the Elbe estuary, and the central German Bight, where highest con-

Fig. 7. Potential larval survival (PLS) versus average water temperature experienced during the spawning season (upper panel: Atlantic cod; lower panel: sprat). The symbols indicate the respective spawning area (Areas I–IV, see Fig. 1), and lines having different shades of grey denote each of the simulated years (black: 1990; dark grey: 1992; light grey: 1996). (Insert 1 and 2) North Sea-wide mean PLS in each spawning month for the 3 years.



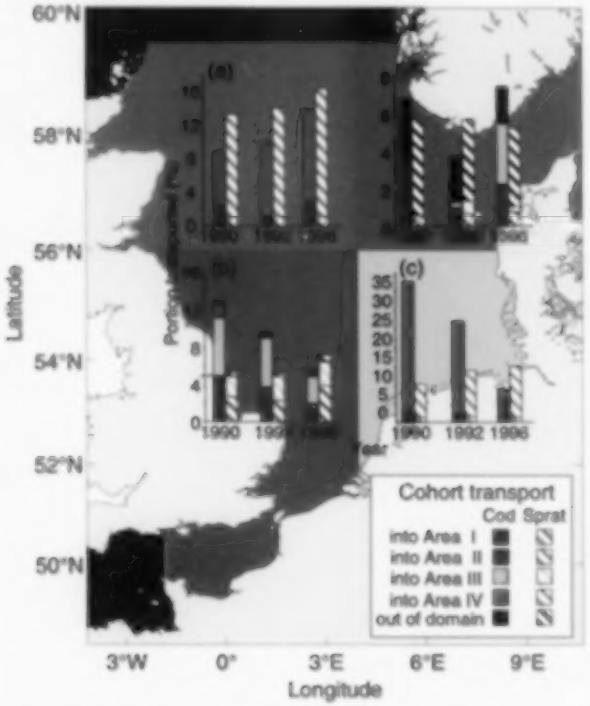
centrations of cod eggs were normally found within frontal zones (Munk et al. 2009). Interestingly, most cod spawning areas determined from that (2004) survey agreed well with historical records of active spawning grounds (Fox et al. 2008) and include areas where genetic differences between spawning populations have been identified (Hutchinson et al. 2001). Besides their genetic dissimilarity, other studies have reported differences in spawning characteristics of cod at different North Sea spawning sites that could potentially influence PLS (e.g., International Council for the Exploration of the Sea 2005; Harrald et al. 2010). For example, cod in the German Bight have a later spawning period (February–May) than cod in the Southern Bight (January–April) (International Council for the Exploration of the Sea 2005), which, according to our results, would increase the annual PLS of cod progeny in the former area.

Although the spatial extent of cod spawning also agreed well with our model-based estimates of PSG (e.g., little spawning activity in the central and northwestern part of the North Sea; Fox et al. 2008), the spatial complexity of observed spawning pockets was not captured by our model system. It appears as though "realised" spawning areas by cod do not reflect all of the areas where spawning could potentially result in high levels of early life stage survival and that additional factors contribute to the choice of spawning areas by this demersal species. For example, cod are known to avoid spawning in turbid waters and have an affinity towards spawning in areas with specific topographic characteristics (Brander 1994; Begg and Marteinsdottir 2002; Rindorf and Lewy 2006). Our model did not include these habitat features. Regardless, the general agreement between observed spawning grounds and modelled PSGs in both sprat and cod help validate our model approach, since spawning grounds utilized by these species in the North Sea were those projected in our model system to promote increased survival of early life stages (exogenously feeding larvae).

Larval survival: detecting relevant processes

The influence of differences in life history strategy and early life stage physiology on the relative impacts of environmental factors was evident from a comparison of the results of our simulations for North Sea cod and sprat. A critical factor influencing survival was the match or mismatch of first-feeding larval fish with their prey (Cushing 1990). A priori to understanding match–mismatch dynamics occurring in the field, a thorough examination of the interrelationships between physical environmental factors and the onset of zooplankton production is required. Unlike temperate lakes where phenological changes in primary and secondary production are often tightly coupled to changes in water temperature via changes in winter ice cover (Weyhenmeyer et al. 1999; Weyhenmeyer 2001), long-term observations in the North Sea at Helgoland Roads (located in our Area III) indicated that even in the coldest years (e.g., 1996), sea ice cover was absent and the dynamics (phenology and biomass) of the spring phytoplankton bloom were comparable to those observed after warmer winters (Wiltshire and Manly 2004). Those finding agree well with our NPZD model estimates, indicating no phenological

Fig. 8. Transport processes impacting nonfeeding developmental stages in Atlantic cod and sprat in the North Sea. The bars indicate the percentage of individuals that left each spawning area (*a*–*d*) (Areas I–IV, see Fig. 1) prior to exogenous feeding. The colours represent the area within which the larvae started to feed (colour code is given by the background colour of each of the four areas). Black indicates the percentage of larvae that were transported out of the model domain.



shifts in the timing of zooplankton production in the German Bight despite relatively large differences in mean winter water temperatures among the 3 years examined here.

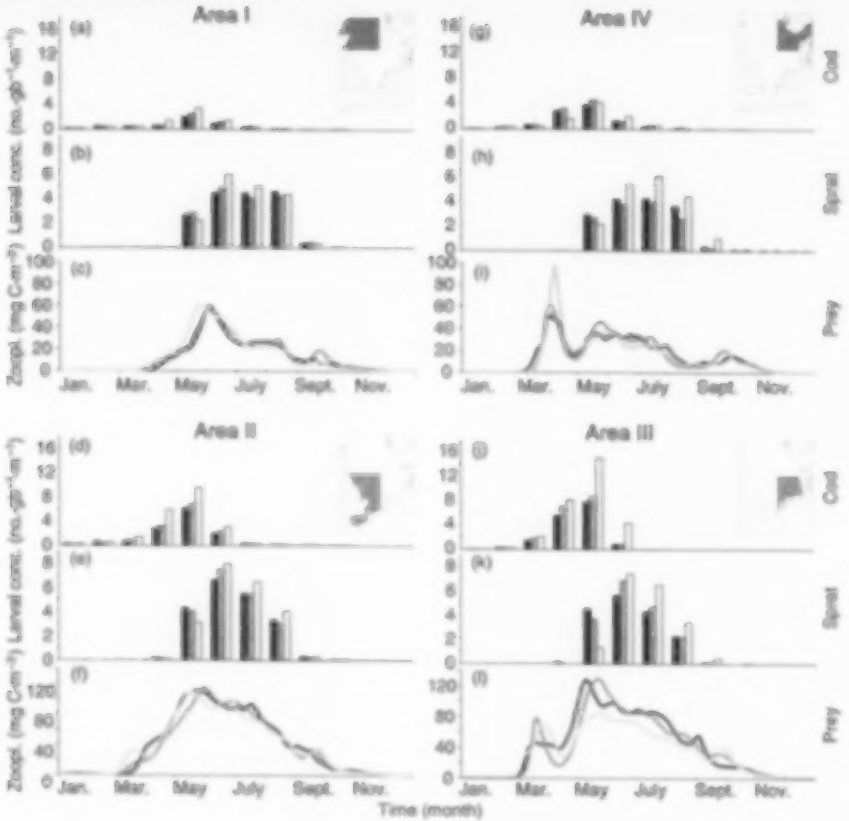
In the North Sea, cod spawn during the winter and early spring (January–April) prior to the spring zooplankton bloom, and therefore their progeny (eggs and larvae) can be exposed to both cold water temperatures and also unfavourable feeding conditions. At typical North Sea winter water temperatures (<8 °C), our IBM estimated that at least 5 mg C·m^{-3} would be required for the survival of cod larvae. Although the comparison of modelled and observed values indicated that the model underestimated zooplankton biomass in those winter months, observed (in situ) zooplankton estimates also suggest that cod larvae may routinely encounter prey fields during the winter that are close to (or fall below) our physiological-based estimate of the threshold needed for survival (CPR: ~1.0–4.0 mg C·m^{-3}; ZISCH: 7.0 mg C·m^{-3}).

Because of longer duration of the time lag between spawning and zooplankton production in cod compared with sprat, match–mismatch dynamics are expected to play a much larger role in controlling larval survival of the former compared with the latter species. This is particularly the case since cod has a somewhat faster rate of development through nonfeeding stages compared with sprat at the same water temperature. On the other hand, first-feeding larval cod have a larger potential prey size spectrum (up to 600 µm) compared with sprat (up to 200 µm) and thus have the ability to survive at lower levels of zooplankton biomass compared with sprat larvae. Since developmental rates and feeding requirements of fish larvae are both strongly temperature-dependent, whereas the timing of secondary production in the North Sea is not, potential survival of larval cod is expected to decline with increasing water temperature. In relatively warm years (e.g., 1990, 1992), development of cod will be relatively rapid, leading to an earlier transition to exogenous (first-) feeding for larvae with relatively higher metabolic requirements, all of which will exacerbate any potential mismatch situation. These mechanisms explain why a negative correlation between potential larval survival and average winter water temperature was observed in the results of our simulations for cod but not for sprat.

Although water temperatures and prey fields interact to place clear, physiological constraints on the survival of marine fish early life stages, our results stress that the ultimate success of larval cohorts in the North Sea will also depend upon changes in transport processes. During the years with strong westerly winds (e.g., 1990 and 1992, the two warmer years simulated in the present study), pelagic eggs and larvae of both cod and sprat were transported away from the spawning area following the general circulation pattern described by Otto et al. (1990). However, a different transport pattern was observed in the drift trajectories of cod eggs and larvae during the exceptionally cold year (1996). In that year, a higher proportion of larvae was retained within favourable feeding areas. Based on positive correlations between the North Atlantic Oscillation (NAO) and water temperature (Becker and Pauly 1996) and wind stress (Siegismund and Schrum 2001), colder years are expected to have lower dispersal and a higher retention of larvae within spawning areas. Moreover, these colder years also delay the timing of first feeding by cod, thus acting to increase the temporal match of larvae with suitable prey. In this manner, temperature, prey, and transport mechanisms interact to influence spatiotemporal patterns in PLS in North Sea cod.

For sprat, our model system projected no interannual differences in PLS or correlation between PLS and temperature. However, our results suggested that first-feeding sprat larvae require relatively high levels of zooplankton biomass for survival compared with cod. This physiological characteristic likely restricts the spatiotemporal occurrence of successful larval sprat cohorts (and thus the spawning of adults) to places and times coinciding with high zooplankton biomass. The highest levels of zooplankton biomass correspond to well-mixed and transitional (frontal) zones between well-mixed and seasonally stratified waters in the southern North Sea (e.g., LeFèvre 1987). Our model suggests that interannual differences in PLS in sprat are most likely related to the position and strength of tidal-mixing fronts (e.g., Munk 1993; Daewel et al. 2008*a*). Frontal residence might increase prey concentrations experienced by sprat, but it would also increase the potential for mortality via predators targeting accumulations of larvae and their zooplankton prey (Floeter 2005). Although predation was not included in our model simulations, we suggest that variability in predation pressure

Fig. 9. Simulated larval concentration vs. time (month) for Atlantic cod and sprat as well as the seasonal dynamics of mean (ECOSMO simulated) zooplankton biomass versus time (days) for Areas I–IV (see insert maps). Years are indicated by different shading of bars and lines (black: 1990; dark gray: 1992; light gray: 1996).



(mortality) may explain a larger portion of the interannual variability in landings and recruitment reported for sprat (e.g., Heath 2005; International Council for the Exploration of the Sea 2007) and other small pelagic species that spawn in the late spring and summer such as newly (re-) established populations of European anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in the North Sea compared with bottom-up controls such as mismatch events.

Coupled modelling and marine fish early life stages

One of the assumptions used to set up the model experiments in this study was that cod and sprat larvae were exposed to the general circulation pattern as passive drifters. In the earliest life stages (eggs and yolk sac larvae), this appears to be a reasonable assumption because of limited swimming ability. However, for older larvae, the consideration of vertical (and (or) horizontal) migratory behaviour might be necessary. Although we could not find any evidence in the literature for vertical migration of cod and sprat larvae in the North Sea, evidence exists that the larvae of both species can perform vertical migration in other areas. For example, working in the Baltic Sea, Voss et al. (2007) reported the presence of diel vertical migration behaviour in sprat larvae >10 mm SL in the early 1990s and the absence of this behaviour in the same area in the early 2000s. The two periods were characterized by large changes in key prey species (calanoid copepods in the *Acartia*, *Temora* and *Pseudocalanus* genera) and changes in water temperature. Although it is difficult to know whether those results apply to the North Sea system, those Baltic observations suggest a potential for diel vertical migration in older sprat larvae. Similarly, in cod larvae >9 mm SL, Lough and Potter (1993) reported that individuals were evenly distributed throughout the water column under well-mixed conditions but were concentrated at the thermocline and performed diel vertical migration in stratified conditions on Georges Bank (Northwest Atlantic). Both studies support our assumption that larvae <10 mm SL can be considered passive particles and, since large parts of the North Sea are well mixed throughout the year (particularly the highly productive southern areas), our assumption also appears valid for larger larvae. However, extending the model into the post-larval and juvenile stages will require additional components depicting active movements such as migratory behaviour.

When searching for critical life stages in marine fish larvae, the relationship among ontogenetic changes in foraging ability versus the available prey fields as well as starvation resistance versus growth potential need to be considered. In

sprat larvae, the first-feeding period was considered "critical" because of low feeding success, but suboptimal prey fields of larger larvae (10–15 mm SL) can also hamper growth performance and survival (Voss et al. 2003). In cod larvae, Jordaan and Brown (2003) identified clear trade-offs among body size, growth performance, and starvation resistance. In that laboratory study, ~12 mm SL cod larvae had the highest potential for growth as well as starvation-induced mortality, while, in contrast, first-feeding larvae had a higher potential to withstand periods of prey deprivation (within limits imposed by the timing of complete yolk absorption and the point of no return (Overton et al. 2010). These and studies conducted on other marine fishes (e.g., Bochdansky et al. 2008) reveal that larvae may need to pass through multiple "critical periods" and that relationship between prey field characteristics and vital rates (growth and survival) can often remain dynamic through the early larval and into the late larval and early juvenile periods (Baumann et al. 2007). Thus, extending our coupled (IBM–NPZD) model approach to later life stages is warranted.

The present study provided an example of how a coupled model systems can provide important tools to move beyond mere statistical analyses (correlations) between climate variability (e.g., changes in the NAO index) and changes in the productivity of fishes in the North Sea and elsewhere. Gaining process understanding of historical changes in fish stocks is particularly difficult in the North Sea, a region where large differences exist among species in terms of their life history strategies (Houde 1989), physiological tolerances (Pörtner et al. 2001; Pörtner and Farrell 2008), and (or) key trophodynamic relationships (Rijnsdorp et al. 2009). Our North Sea simulations for cod and sprat included environmental changes in key physical and biological factors as well as species-specific differences in life history (reproductive) strategies and growth physiology of early life stages. Although longer-term (decadal) simulations will ultimately be required to link the mechanisms identified here (match–mismatch and transport dynamics) to variability in climate and recruitment, our results suggest that the likelihood of mismatch events between first-feeding cod larvae and their prey in the North Sea is clearly correlated to changes in climatic conditions. It is important to note that our model system was designed to explicitly test for climate impacts on bottom-up processes. Thus, one cannot conclude that top-down processes (and the effects of climate on those processes) are not also relevant causal factors affecting the vital rates of marine fish early life stages within our model domain (the North Sea).

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Appendix A

Appendix A continues on following pages.

IBM parameterization

All model parameters and the associated units are listed in Table A1.

Table A1. List of parameters and units used in the individual-based model.

Variable	Parameter	Units
H_{ep}	Development rates of eggs	%·day^{-1}
H_{ys}	Development rates of yolk-sac larvae	%·day^{-1}
β	Assimilation efficiency	—
R_A	Active metabolism	μg DM·h^{-1}
k	Activity multiplier	—
α	Angle of visual acuity	°
$CS_{L,i}$	Capture success	—
C_{day}	Daily food consumption	μg·day^{-1}
$N_{L,i}$	Encounter rate	no.·s^{-1}
C	Food consumption	μg·Δt^{-1}
$HT_{L,i}$	Handling time	s
M_D	Larval dry mass	μg
G	Larval growth	mm·Δt^{-1}
GC_{max}	Gut content	μg
GER	Gut evacuation rate	%·h^{-1}
L_S	Larval length	mm
$SS_{L,i}$	Larval swimming speed	mm·s^{-1}
$pl_{i\ max}$	Maximum prey *size*	mm
pl_i	Prey length	mm
m_i	Prey mass	μg
PS	Prey swimming speed	mm·s^{-1}
RD_i	Reactive distance	mm
SDA_{m_i}	Specific dynamic action	—
R_S	Standard metabolism	μg DM·h^{-1}
T	Temperature	°C
Δt	Time interval	s
w	Turbulence-generated velocity difference	mm·s^{-1}
C_{MAX}	Upper limit to food consumption	μg
V	Velocity component of contact rates	mm·s^{-1}
γ	Oxycaloric equivalent	cal μL O_2^{-1}
χ	Calorie to microgram mass conversion factor	μg DM·cal^{-1}

Note: 1 calorie = 4.185 J.

IBM: nonfeeding stages

The duration of the nonfeeding life period is temperature-dependent and was calculated using empirically derived functions (Table A2).

Table A2. Equations for developmental rates during nonfeeding life stages (eggs, yolk-sac larvae).

				Citation	
Eq.	Variable	Sprat	Atlantic cod	Sprat	Atlantic cod
A.1	H_{ep}	$1.30\,T^{1.26}$	$\frac{1}{10^{(-0.0267T^2+0.9662T-7.7)}}$	Thompson et al. 1981	Geffen et al. 2006
A.2	H_{ys}	$0.27\,T^{1.495}$	$e^{(-5.6+0.22T)}$	Alshuth 1988	Jordaan and Kling 2003

IBM: food consumption

The equations required to simulate larval food consumption are given in Table A3. The encounter rate of larvae with their prey (eq. A.3) depends not only on larval reactive distance (eq. A.3.1) and prey density, but also on larval swimming behavior and turbulence. A cruise predator formulation was used for sprat (see Daewel et al. 2008*b* for details), while cod larvae were considered pause–travel predators, searching for prey during pauses between swimming events. Hence, in the case of cod, prey encounter rates were determined by pause frequency (P_f) and pause duration (P_d) (MacKenzie and Kiørboe 1995). According to Lough et al. (2005), P_d = 1.7 s for small cod (<5.5 L_S) and 1.4 s for larger cod and P_f = 30/60 pauses·s^{-1} and 32/60 pauses·s^{-1}, respectively. Turbulence was included into the expression of encounter rate as described by Evans (1989). The velocity component of contact rates (eq. A.3.3) was composed of the predator swimming speed (eq. A.3.4), the prey speed (eq. A.3.5), and the turbulence-generated velocity difference, which was calculated according to Rothschild and Osborn (1988). Additionally, the encounter rate was multiplied with a turbulence-dependent ingestion probability calculated according to MacKenzie et al. (1994). Feeding was also sensitive to the prevailing light intensity, where the threshold was set to 0.1 lx (~0.017 μE·m^{-2}·s^{-1}) as observed for feeding by herring larvae (Blaxter 1986).

Table A3. IBM equations relevant for larval food consumption of Atlantic cod and sprat and the respective references.

				Citation	
Eq.	Variable	Sprat	Atlantic cod	Sprat	Atlantic cod
A.3	$N_{L_S,t}$	$\frac{1}{2}\,\pi \mathrm{RD}^2 \mathrm{pl}_t\, V$	$\left(\frac{1}{2}\,\pi \mathrm{RD}^2 p_t P_f\right) + \left(\pi \mathrm{RD}^2 p_t P_f P_d\, V\right)$	Letcher et al. 1996	MacKenzie and Kiørboe 1995
A.3.1	RD_t	$\frac{\mathrm{pl}_t}{2\tan\left(\frac{\alpha}{2}\right)}$	$\frac{\mathrm{pl}_t}{2\tan\left(\frac{\alpha}{2}\right)}$	Breck and Gitter 1983	Breck and Gitter 1983
A.3.2	α	$0.0167\, e^{0.14-2.4\ln(L_S)+0.229\left[\ln(L_S)\right]^2}$	$0.0167\, e^{0.14-2.4\ln(L_S)+0.229\left[\ln(L_S)\right]^2}$	Breck and Gitter 1983	Breck and Gitter 1983
A.3.3	V	$\sqrt{\mathrm{PS}^2 \times \mathrm{SS}_{L_S}{}^2 \times 2w^2}$	$\sqrt{\mathrm{PS}^2 \times \mathrm{SS}_{L_S}{}^2 \times 2w^2}$	Evans 1989	Evans 1989
A.3.4	SS_{L_S}	$\frac{101.15}{1+e^{\left[\frac{-(L_S-24.11)}{3.07}\right]}}$	$0.261\, L_S^{\left(1.552\, L_S^{(-0.1)}\right)} - \frac{5.289}{L_S}$	Munk 1992	Peck et al. 2006
A.3.5	PS	$3\,\mathrm{pl}_t$	$3\,\mathrm{pl}_t$	See Daewel et al. 2008*a*	See Daewel et al. 2008*a*
A.4	$\mathrm{CS}_{L_S,t}$	$1.1 - \left(a \times \frac{\mathrm{pl}_t}{L_S}\right)$	$1.1 - \left(a \times \frac{\mathrm{pl}_t}{L_S}\right)$	Munk 1992	Munk 1992
A.4.1	a	$\frac{3.1\, L_S}{\mathrm{pl}_{t,\max}}$	$\frac{3.1\, L_S}{\mathrm{pl}_{t,\max}}$	Daewel et al. 2008*a*	Daewel et al. 2008*a*
A.4.2	$\mathrm{pl}_{t,\max}$	$\frac{1524.9}{1+\left(\frac{L_S}{12.5}\right)^{-7.55}}$	$\frac{1.2936}{1+e^{-0.2\left(L_S-0.8963\times 2900\right)}}$	Daewel et al. 2008*a*	Unpublished data (see text)
A.5	$\mathrm{HT}_{L_S,t}$	$e^{0.264\times 10^{-7.0(0)}\left(\frac{L_S}{T_t}\right)}$	$e^{0.264\times 10^{-7.0(0)}\left(\frac{L_S}{T_t}\right)}$	Walton et al. 1992	Walton et al. 1992
A.6.1	C_{MAX}	$1.315\, M_D^{0.83} \times 2.872^{\left[\frac{T_{\mathrm{ref}}-20}{10}\right]}$	—	Daewel et al. 2008*a*	—
A.6.2	$\mathrm{GC}_{\max}$	—	$3.24 + 0.064\, M_D$	—	Lough et al. 2005
A.6.3	GER	—	$1.792\, L_S^{-0.228} \times Q_{10}{}^{\left(\frac{T_{\mathrm{ref}}-T}{10}\right)}$	—	Peck and Daewel 2007

Capture success (eq. A.4) has been parameterized as a function of prey length and larval length (Munk 1992) and differs for Atlantic cod and sprat in the formulation of the maximum prey size versus larval size (eq. A.4.2). This formulation was based upon measurements made of the prey in gut contents of sprat (Voss et al. 2003; Dickmann et al. 2007) and Atlantic cod (G. Lough, Northeast Fisheries Science Center, NMFS, NOAA, Woods Hole, MA 02543, USA, unpublished data).

In the cod IBM, the majority of the parameter estimates was the same as utilized by Lough et al. (2005), including parameterizations needed for the foraging and growth submodule. One parameter that prevented overfeeding (gut evacuation rate, GER) needed to be modified so that modelled growth matched observations of larval cod growth over a broad range of temperatures (Otterlei et al. 1999). GER was adapted from a generalized formulation published by Peck and Daewel (2007) (eq. A.6.3) and included a Q_{10} of 3 and a threefold increase in GER during feeding, adjustments well within the range of values observed for the larvae of a number of different species (see Peck and Daewel 2007). In the sprat IBM, a maximum consumption parameter ($C_{\max}$) (eq. A.6.1) was utilized (instead of GER) to prevent overfeeding and unrealistically high growth rates (see Daewel et al. 2008*b*).

IBM: metabolic losses and length growth

Equation for larval mass–length relationships (eq. A.11) and metabolic losses including assimilation efficiency (eq. A.7), specific dynamic action (eq. A.8), and standard and active metabolic rates (eqs. A.9 and A.10) are given in Table A4.

Table A4. Model equations for metabolic losses and the mass–length relationship for Atlantic cod and sprat.

				Citation	
	Variable	Sprat	Atlantic cod	Sprat	Atlantic cod
A.7	β	$0.7\left[1-0.3\,e^{-0.003(M_D-M_{D_{\text{hatch}}})}\right]$	$0.7\left[1-0.4\,e^{-0.003(M_D-50)}\right]$	Buckley and Dillmann 1982	Lough et al. 2005
A.8	SDA_{m_i}	$0.11+4.91\times10^{-3}\times m_i$	0.35	See Daewel et al. 2008*a*	Lough et al. 2005
A.9	R_s	$b\times0.00272\times M_D^{0.80}\times2.57^{\left[\frac{T-10}{10}\right]}$	$b\times0.00114\times M_D^{(1.02800-0.00774\times\ln M_D)}\times e^{[(0.10720-0.00320\times\ln M_D)\times T]}$	Kiørboe et al. 1987	Lough et al. 2005
A.9.1	b	$\gamma\times\chi$	$\gamma\times\chi$	Hinckley et al. 1996	Hinckley et al. 1996
	γ	0.00463	0.00463	Brett and Groves 1979	Brett and Groves 1979
	χ	227.0	227.0	Theilacker and Kimball 1984	Theilacker and Kimball 1984
A.10	R_a	$k\times R_s$	$k\times R_s$	—	—
A.10.1	k	$k=\begin{cases}1.9+0.0076m_i & \forall m_i\le800\text{ g}\\2.5 & \forall m_i>800\text{ g}\end{cases}$	$k=\begin{cases}1.4 & \forall L_S<5.5\text{ mm}\\2.5 & \forall L_S\ge5.5\text{ mm}\end{cases}$	Beyer and Laurence 1980	Lough et al. 2005
A.11	L_s	$3.928\,M_D^{0.199}$	$1.935\,M_D^{0.247}$	Peck et al. 2005	Lough et al. 2005

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Synchrony in marine growth among Atlantic salmon (*Salmo salar*) populations

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Abstract: More synchronous growth was observed between close, than more distantly separated populations of Atlantic salmon (*Salmo salar*), during both the first and the second year at sea. The marine growth of seven Norwegian populations, located between 60°N and 70°N, were correlated with sea surface temperatures (SSTs) in the Barents Sea, the Norwegian Sea, and the North Sea, and it was found that growth correlated best with the water temperatures in the area located closest to their home river. Growth was also compared with three broad-scale climate indices (North Atlantic Oscillation (NAO), Atlantic Multidecadal Oscillation, and subpolar gyre), with the strongest relationship occurring with the NAO index. However, SSTs explained more of the variability than the climatic indices did. Growth increment for the first year, but not the second year, was higher for southern than northern populations, mainly because of later smolt migration to sea in the north, and hence, a shorter growth season. For multi-sea-winter fish, all populations except one had a negative trend in growth with years for both the first and the second year at sea. For the second year at sea, this was most pronounced after the beginning of the 1980s. This is in accordance with the negative trend in pre-fishery abundance of adult salmon during the same period.

Résumé : On observe plus de croissance synchronisée entre les populations adjacentes que plus éloignées chez le saumon atlantique (*Salmo salar*), tant durant la première que la seconde année en mer. Nous avons mis en corrélation la croissance en mer de sept populations norvégiennes, établies entre 60°N et 70°N, et les températures de surface de la mer (SST) dans la mer de Barents, la mer de Norvège et la mer du Nord; la croissance est le mieux corrélée avec les températures des sites situés le plus près de leur rivière natale. Nous avons aussi comparé la croissance avec trois indices climatiques à grande échelle (l'oscillation nord-atlantique (NAO), l'oscillation atlantique multidécennale et le tourbillon subpolaire) et la relation la plus forte s'établit avec l'indice NAO. Cependant, les SST expliquent une plus grande partie de la variabilité que les indices climatiques. L'incrément de la croissance pour la première année, mais non pour la seconde, est plus élevé pour les populations du sud que pour celles du nord, surtout à cause de la migration plus tardive des saumoneaux vers la mer dans le nord et ainsi, de la période de croissance plus courte. Chez les poissons qui passent plusieurs hivers en mer, toutes les populations, sauf une, affichent une tendance négative de la croissance en fonction des années, tant pour la première que pour la deuxième année en mer. Pour la deuxième année en mer, la tendance est plus prononcée après le début des années 1980. Cela concorde avec la tendance négative dans l'abondance des saumons adultes pendant la même période.

[Traduit par la Rédaction]

Introduction

Spatial synchrony in animal population fluctuations across space has puzzled biologists for centuries (Moran 1953; Ranta et al. 1997; Ripa and Ranta 2007). Such synchrony may arise from exogenous factors such as temperature, rainfall, or other meteorological elements, a phenomenon known as the "Moran effect" (Moran 1953; Grenfell et al. 1998). However, other mechanisms may cause synchrony, such as dispersal among populations that reduce the size of relatively large populations and increase that of relatively small ones, or trophic interactions that cause spatial synchrony between the predator population and the prey species (Liebhold et al. 2004). Synchrony in population sizes and recruitment have also been found in many fish species (e.g., Fromentin et al. 2000; Tedesco and Hugueny 2006; Nunn et al. 2007), including salmonids (Friedland et al. 1998; Niemelä et al. 2004; Pyper et al. 2005). Peterman et al. (1998)

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examined spatial patterns among survival rate indices and found positive covariation among stocks of sockeye salmon (*Oncorhynchus nerka*) in the northeast Pacific Ocean at regional scales, but not at a larger, ocean-basin scale. Similar results are also found for pink salmon (*Oncorhynchus gorbuscha*) (Pyper et al. 2001) and chum salmon (*Oncorhynchus keta*) (Pyper et al. 2002). In the northeast Atlantic Ocean, synchrony in recruitment in Atlantic salmon (*Salmo salar*) has been reported for two sets of geographically close pairs of populations in Scotland and South Norway (Friedland et al. 1998) and in the Barents Sea (Niemelä et al. 2004). The synchrony documented in these studies suggests that survival rates are affected by similar environmental processes that operate primarily at confined spatial scales (Pyper et al. 2005).

Atlantic salmon spend the first 1–7 years of their life cycle in fresh water, although most of their somatic growth occurs during the marine phase. While the different populations are physically separated during the freshwater phase, their areas of distribution at sea may overlap (Hansen and Jacobsen 2003). The smolts migrate to feeding areas at sea where they grow rapidly from 10–50 g to several kilograms. They leave their natal rivers in spring, earlier in the south than in the north (Hvidsten et al. 1998). After leaving the river, they migrate directly into off-shore areas (Thorstad et al. 2007), and distribute over large areas of the North Atlantic (Holm et al. 2004). In the marine phase, they feed in surface waters, and mainly occupy the upper 30 m of the water column, but with some occasional dives to larger depths (Holm et al. 2004). At the population level, the distribution at sea is not known, but fish originating from several rivers have been shown to be present in the same areas (Hansen and Jacobsen 2000; Hansen and Jacobsen 2003; Dadswell et al. 2010). The distribution at sea probably depends on a combination of factors such as food availability, water temperature, and currents, as well as on genetic components that govern population-specific navigation systems (Hansen and Quinn 1998; Holm et al. 2004).

Over the last three decades, the abundance of Atlantic salmon has declined over most of its distribution area, in spite of reductions in fishing pressure and measures to protect critical habitats (Friedland et al. 2009*b*). The recruitment pattern of salmon has been associated with marine growth, with increased sea survival from enhanced growth (Friedland et al. 2000; Peyronnet et al. 2007; McCarthy et al. 2008). Further, enhanced growth has been associated with favorable temperature conditions, both in the early post-smolt period (Dannevig 1949; Friedland et al. 1998; Hvidsten et al. 2009) and later in the marine phase (Reddin and Shearer 1987; Friedland et al. 2000). Therefore, we suggest that regional and seasonal, as well as annual variations in sea temperatures in the main distribution area of an Atlantic salmon population will be reflected in the growth pattern stored in their scales. Hence, we hypothesize that more similar marine growth patterns will be found in salmon populations from adjacent rivers than in more distant populations. This was tested by analyzing marine growth from scale samples of adult Atlantic salmon collected systematically for 18–46 years in seven Norwegian rivers, located between 60°N and 70°N.

Materials and methods

Populations

The seven populations of Atlantic salmon studied originated from rivers along the Norwegian coast between 60°N and 70°N (Fig. 1). According to the category system of Porter et al. (1986) they are all Type III populations, i.e., with some individuals maturing at each of the three sea-age groups: grilse (1SW), two-sea-winters (2SW), and three-sea-winters (3SW). Four-sea-winter (4SW) spawners were also present in all populations. In all populations, most of the grilse were males, whereas most of the multi-sea-winter (MSW) salmon were females. Salmon from all rivers except Drammenselva were wild, whereas a large part of Drammenselva salmon were local fish stocked as juveniles, mainly fry and under-yearlings.

Growth

Scales from adult Atlantic salmon were collected annually during the recreational fishing season in the rivers (June–September) for 18–46 years (Table 1; Fig. 1). The scales were sampled from an area close to the lateral line between the dorsal and adipose fins. Annual growth increments in length were estimated by back-calculation, using the Dahl–Lea method (direct proportion formula through the origin) developed by Lea (1910), and described in detail in Francis (1990):

$$(1) \qquad L_i = (S_i/S_c)L_c$$

where L_c and S_c are body length and scale radius at capture, respectively, and L_i and S_i are the corresponding measurements at the time of formation of the ith scale mark. Using this method made larger data series available for analysis. This method was tested against the Fraser–Lee method (Lee 1920), using a constant c:

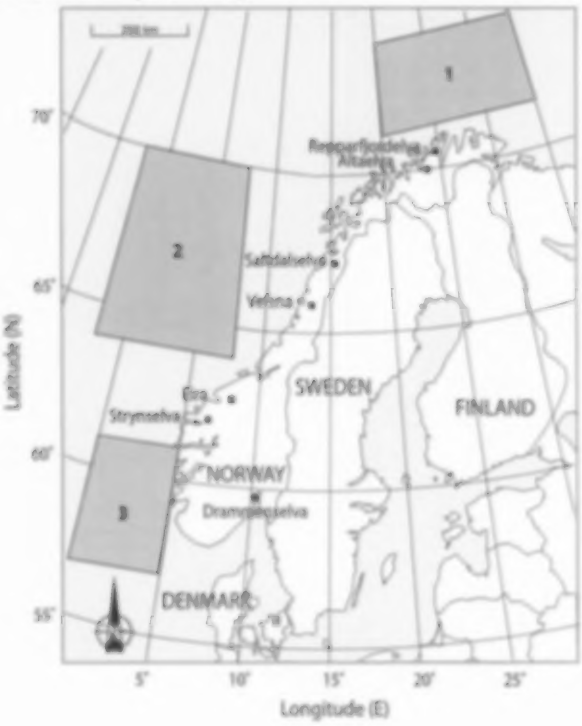
$$(2) \qquad L_i = c + (L_c - c)(S_i/S_c)$$

with a subset of scales from the River Repparfjordelva where data on scale radius measurements were available. The trends obtained by the Dahl–Lea and Fraser–Lee methods on the subset of scale samples were the same (A.J. Jensen, unpublished data), and therefore the bias associated with the extrapolation of the Dahl–Lea method is not expected to affect the overall trends presented here, but the magnitude of the first year growth.

The first year growth at sea was estimated based on the length increment from seaward migration as smolt to the end of the first sea winter annulus. Repeat spawners were excluded from the material. Sample size within a year and sea age group (1SW or MSW) varied between 10 and 526 (average 68). Individual fish in the studied rivers were analyzed based on the year of smoltification.

In four rivers, the time when smolts migrated to sea has been studied for several years (Johnsen et al. 1997; Hvidsten et al. 1998; Jensen et al. 2009), and the median date of smolt migration is provided (Table 1). For the other three

Fig. 1. Map with the three sea surface temperature (SST) areas (1, Barents Sea; 2, Norwegian Sea; 3, North Sea) and the seven rivers included in the present study.



rivers, median date has been stipulated by using corresponding information from the nearest river with available information (Hvidsten et al. 1998; Jensen et al. 2009; T. Forseth, Norwegian Institute for Nature Research (NINA), Trondheim, Norway, unpublished data). The distance used to impute the median date of smolt migration was 80, 383, and 310 km for the rivers Repparfjordelva, Stryneselva, and Drammenselva, respectively.

Standardized mass-specific growth rate (Ω%) was calculated according to Ostrovsky (1995):

$$(3) \qquad \Omega = \frac{M_t^b - M_0^b}{b \times t} \times 100$$

where M_0 and M_t are the respective body mass (g) at the beginning and end of each period, b is the allometric mass exponent for the relation between specific growth rate and body mass, estimated at 0.31 for Atlantic salmon by Elliott and Hurley (1997), and t is the time period (days). For the first year at sea, t was set to be the number of days from seaward migration to the end of the year, and for the second year at sea the whole calendar year (360 days) was used.

Pre-fishery abundance

Normalized pre-fishery abundance for the smolt years 1970–2003 of the northern subcomponent of the European salmon stock complex (1SW and 2SW salmon) was extracted from Fig. 3*a* in Friedland et al. (2009*b*).

Oceanographic data

Mean monthly SST temperatures from the Met. Office Hadley Centre (HadISST) with 1° × 1° horizontal resolution (Rayner et al. 2003) are spatially averaged over three different areas (Fig. 1) for the period 1951–2002. The three areas, which cover the distribution area of Norwegian Atlantic salmon, are parts of the Barents Sea (St. 1, 20°–35°E, 71°–74°N), the Norwegian Sea (St. 2, 2°W–8°E, 64°–70°N), and the North Sea (St. 3, 0°–5°E, 57°–61°N). The monthly time series of sea surface temperature (SST) for these three areas were compared with marine growth of the seven salmon populations.

The time series of marine growth of Atlantic salmon were compared with three broad-scale climate indices: the North Atlantic Oscillation (NAO), the Atlantic Multidecadal Oscillation (AMO), and the subpolar gyre.

The NAO index is based on the difference in normalized sea level pressure between Lisbon, Portugal, and Reykjavik, Iceland (Hurrell 1995), which is known to affect the physical environment and biological populations across the North Atlantic Ocean (Hurrell et al. 2003; Furevik and Nilsen 2005). We used the winter index (December through March), because the fluctuations in atmospheric pressure are of greatest amplitude at that time of the year. For the Nordic Seas, a higher NAO index is associated with a general sea surface warming along the eastern margin, with a warming in the Barents Sea, the North Sea, and the Baltic Sea, and a cooling in the southwestern part of the Norwegian Sea (Furevik and Nilsen 2005). However, the NAO index does not only reflect changes in SST, but also a large number of different mechanisms, such as wind speed and direction, heat flux, ocean circulation etc. (Furevik and Nilsen 2005). A positive NAO index will be associated, for instance, with an intensification of the eastern branch of the Norwegian Atlantic Current (Orvik et al. 2001).

We used the AMO index from Enfield et al. (2001), where monthly SST data are averaged over the North Atlantic, 0°–70°N, and then detrended. This index represents large-scale SST variations in the North Atlantic without anthropogenic effects, because the time series is detrended. On a multidecadal scale, it influences the summer climate of both North America and western Europe (Sutton and Hodson 2005), and Skagseth et al. (2008) demonstrated the similarity between the AMO index and the decadal temperature variations in the Kola section.

The subpolar gyre in the North Atlantic is defined by the ocean circulation in the North Atlantic, and an index of its strength is based on spatially averaged sea surface height anomalies in the North Atlantic. The yearly gyre index values are similar to Hátún et al. (2005), which are based on Häkkinen and Rhines (2004). Regarding the Norwegian Sea, the strength of the gyre affects the properties of the inflowing Atlantic water to the Norwegian Sea, where the decreased/increased strength of the gyre allows more/less of the warmer and saline eastern North Atlantic water to enter the Norwegian Sea (Häkkinen and Rhines 2004; Hátún et al. 2005).

Statistical tests

We performed Mantel tests (Mantel 1967) using the function Mantel from the package Ecodist in R (version 2.10.1,

Table 1. Rivers sampled for Atlantic salmon scales, latitude and longitude of the river mouth, sampling period, sample size, back-calculated smolt size (mm ± SE), and median smolt migration date.

River	Latitude (°N)	Longitude (°E)	Sampling period	Sample size	Back-calculated smolt size	Median smolt migration date
Repparfjordelva	70°27′	23°54′	1959–2003	6726	148.0±0.28	(1 July)
Altaelva	69°58′	23°23′	1982–2003	8520	135.8±0.22	25 June
Saltdalselva	67°06′	15°25′	1977–2003	1390	144.4±0.55	5 June
Vefsna	65°51′	13°12′	1954 & 1969–1985	1607	134.8±0.54	25 May
Eira	62°41′	8°10′	1987–2003	1028	132.6±0.63	13 May
Strynselva	61°54′	6°43′	1954–1957 & 1983–2003	1243	135.5±0.63	(13 May)
Drammenselva	59°45′	10°14′	1983–2003	2111	157.0±0.58	(4 May)

Note: Dates in parentheses are stipulated according to information from neighbouring rivers.

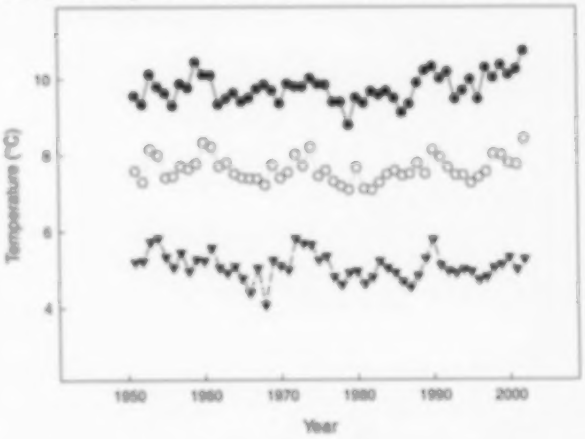
The R Development Core Team 2010). We omitted the River Vefsna from these tests because correlation coefficients for growth could not be obtained, owing to few overlapping years with two other rivers.

To correct for multiple tests of the same null hypothesis we used the sequential Bonferroni procedure (Holm 1979) to adjust the significance level.

Results

Annual mean temperatures (±SE) were 5.08 ± 0.050, 7.63 ± 0.045, and 9.76 ± 0.052 °C for St. 1, St. 2, and St. 3, respectively. Annual mean temperatures at all three stations were significantly correlated (St. 1 ~ St. 2: Pearson correlation, $r = 0.630$, $n = 52$, $p < 0.001$; St. 1 ~ St. 3: $r = 0.407$, $n = 52$, $p = 0.003$; St. 2 ~ St. 3: $r = 0.665$, $n = 52$, $p < 0.001$). There was no significant trend in annual mean temperatures during the time period for St. 1 ($r = -0.238$, $p = 0.089$) or St. 2 ($r = 0.016$, $p = 0.910$), while SST increased with time at St. 3 ($y = 0.0073x - 4.60$, $r = 291$, $p = 0.036$) (Fig. 2).

Fig. 2. Time series of annual mean sea surface temperature (SST) at St. 1 (inverted fillled traingle (▼) Barents Sea), St. 2 (open circle (○) Norwegian Sea), and St. 3 (filled circle (●) North Sea).



For all seven populations, the mean growth increment in length for the first year at sea was significantly smaller for 1SW fish than for 2SW and 3SW fish, while 2SW and 3SW fish were not significantly different (repeated measures analysis of variance (ANOVA), $F_{[2,12]} = 32.89$, $p < 0.001$, Bonferroni post hoc tests 1SW vs. 2SW: $p = 0.002$, 1SW vs. 3SW: $p = 0.003$, 2SW vs. 3SW: $p = 0.373$) (Table 2). For 1SW fish, growth for the first year at sea of males was significantly higher than that of females (growth standardized within populations: males, mean = 0.027, SE = 0.01, $n = 10\,044$; females, mean = –0.13, SE = 0.025, $n = 1\,585$; $t = 5.96$, $p < 0.001$). Therefore, all further analyses were carried out separately for 1SW and MSW fish.

The mean growth increment for the first year at sea of 1SW and MSW fish were significantly correlated for six of the seven populations (Table 3). For all sea ages, mean growth increment for the first year at sea was lowest in the population located furthest to the north (Repparfjordelva), and increased successively towards the south, with the Drammenselva population having the highest growth increment (Table 2). The growth increment for the first year at sea was significantly correlated with latitude of population origin, both for 1SW, 2SW, and 3SW fish, with a latitudinal trend of decreasing growth from south to north (Fig. 3*a*). However, for the growth increment for the second year at sea, the correlation was the opposite, with increasing growth towards the north, significantly for 3SW ($p = 0.025$), but not for 2SW fish ($p > 0.05$) (Fig. 3*b*). No significant trend was found between growth increment for the third year at sea and latitude (Fig. 3*c*).

The significant relationship that was found between latitude and growth-in-length for the second year at sea for 3SW fish (Fig. 3*b*) might be misleading, because fish from lower latitudes had become larger at the start of the second year at sea than those further to the north. Therefore, the standardized growth rate in mass was also estimated (Ostrovsky 1995), with the average condition factor of fish being equal to 0.90 (Jacobsen and Hansen 2001). The relationship between latitude and standardized growth rate in mass for 3SW fish was also significant ($r = 0.823$, $p = 0.023$). A similar test of the relationship between latitude and standardized growth rate in mass during the second year at sea of 2SW fish was not significant ($p > 0.05$).

Smolts enter the sea later in the season the further north their rivers were situated, with a difference of about 8 weeks between the southernmost and northernmost rivers (Table 1). For all sea ages (1SW, 2SW, and 3SW) and populations, the mean growth increment for the first year at sea was significantly negatively correlated with the median date of the smolt migration (Figs. 4*a*–4*c*). Daily growth rates during

Table 2. Growth increment for the first year at sea (mm ± SE) for Atlantic salmon of different sea ages in the seven rivers.

Sea age	Repparfjordelva	Altaelva	Saltdalselva	Vefsna	Eira	Strynselva	Drammenselva
1SW	253.6±0.48	281.0±0.53	289.4±1.38	309.4±1.28	300.9±1.76	301.6±2.70	315.4±1.30
2SW	265.7±1.47	296.6±1.37	309.8±2.01	324.9±1.72	328.6±2.51	341.0±2.41	348.0±1.89
3SW	278.6±1.15	295.9±0.58	316.6±1.93	320.9±1.93	335.8±2.99	339.3±1.35	361.6±3.69
4SW	278.9±3.86	288.4±2.16	325.6±7.63	327.1±9.28	333.9±9.21	332.7±3.48	

Note: SW, sea winter(s).

Table 3. Correlation between annual mean growth increment for the first year at sea of 1SW salmon and MSW salmon of the same smolt year class.

River	*r*	*n*	*p*
Repparfjordelva	0.894	42	<0.001
Altaelva	0.861	21	<0.001
Saltdalselva	0.699	19	0.001
Vefsna	0.842	12	<0.001
Eira	0.673	14	0.008
Strynselva	0.419	10	0.228
Drammenselva	0.599	20	0.005

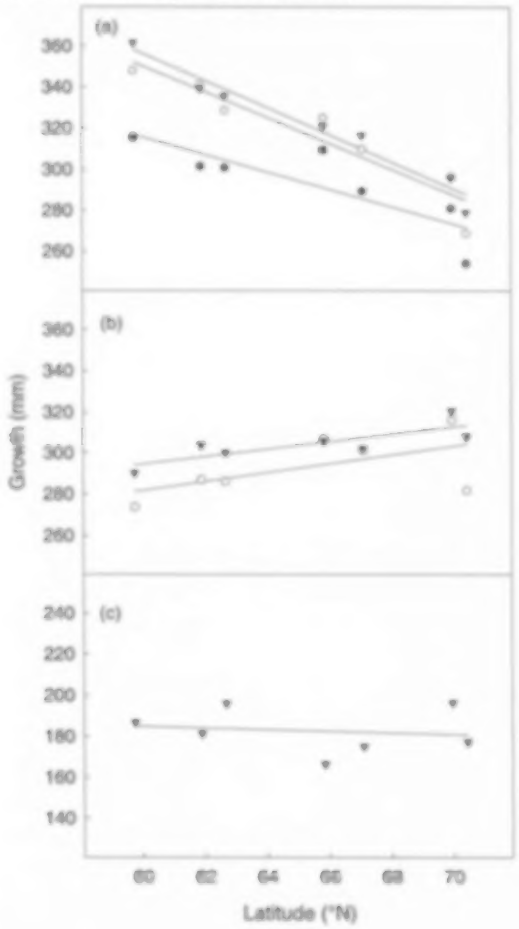
Note: *r*, Pearson correlation; *n*, number of cases (years); *p*, level of significance.

the first year at sea were not significantly different for 1SW, 2SW, or 3SW fish (Figs. 4*d*–4*f*).

Both first and second year growth increments at sea varied among years and populations (Fig. 5). For 1SW fish, first year growth decreased significantly during the study period in one of the seven populations (Vefsna, $r = -0.573$, $n = 14$, $p = 0.032$). For MSW fish, a similar significant decrease was observed in three populations (Saltdalselva: $r = -0.432$, $n = 23$, $p = 0.039$; Strynselva: $r = -0.508$, $n = 21$, $p = 0.019$; Drammenselva: $r = -0.435$, $n = 22$, $p = 0.043$). For the second year at sea, growth decreased significantly during the study period, in three populations: the two in the far north (Repparfjordelva, $r = -0.428$, $n = 43$, $p = 0.003$; Altaelva, $r = -0.605$, $n = 25$, $p < 0.001$), and the southernmost river (Drammenselva, $r = -0.727$, $n = 21$, $p < 0.001$). The most pronounced reduction took place after about 1980 in the longest time series (Repparfjordelva) (Fig. 5*h*). If just the period after 1980 was considered, the trend of decreasing growth with time during the second year at sea was negative in all populations. In addition to those in the rivers Repparfjordelva, Altaelva and Drammenselva, the decrease in Strynselva was also highly significant (Fig. 5*m*, $r = -0.860$, $n = 19$, $p < 0.001$).

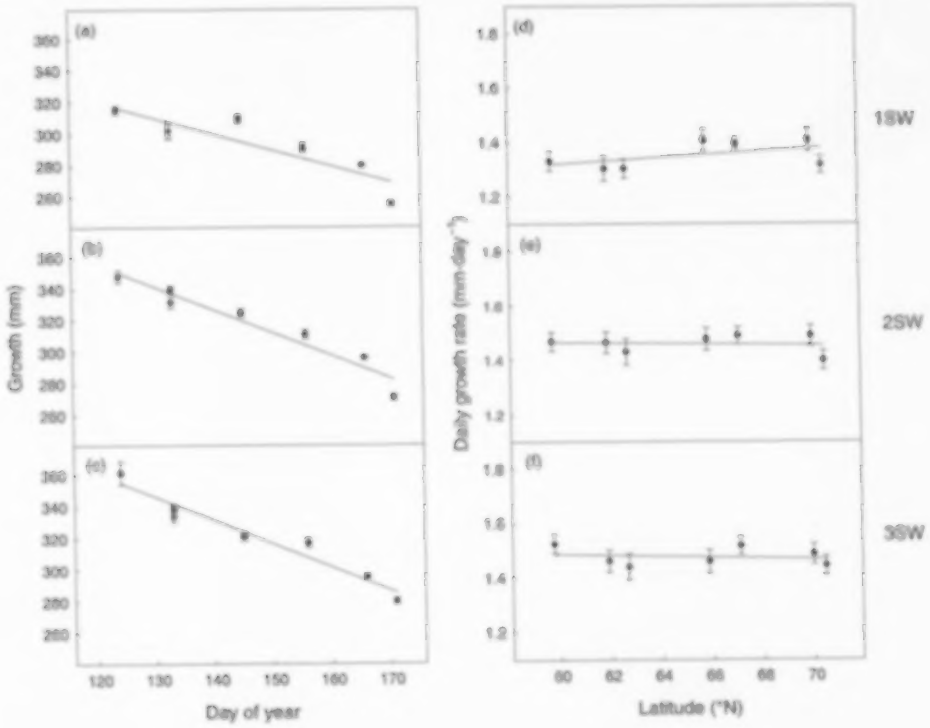
More similar (synchronous) variation between years in mean growth increment for the first year at sea was observed between populations from close rivers than from more distant ones (Mantel tests, $r = -0.55$, $p = 0.009$ for 1SW and $r = -0.64$, $p = 0.009$ for MSW fish, Fig. 6). In the two populations in the far north (Repparfjordelva and Altaelva), first year growth was highly correlated both for 1SW and MSW fish (1SW: $r = 0.912$, $n = 22$, $p < 0.001$; MSW: $r = 0.799$, $n = 25$, $p < 0.001$). The growth of the Repparfjordelva population was also significantly correlated with the rivers Saltdalselva, Vefsna, and Eira, but not with the southernmost rivers. In the southernmost population (Drammenselva), growth correlated significantly with populations in south Norway, but not with the four most northerly populations.

Fig. 3. Relationship between mean growth increment at sea (mm) (filled circle (●), 1SW; open circle (○), 2SW; filled inverted triangle (▼), 3SW) and latitude of the river outlet of the seven Atlantic salmon populations, (*a*) first year at sea (i.e., from smolt migration to the end of the first winter [$p < 0.05$ for all regressions]), (*b*) the second year at sea ($p > 0.05$ for 2SW, $p < 0.05$ for 3SW), and (*c*) the third year at sea ($p > 0.05$).



For the second year at sea (only MSW fish) the mean growth increment was significantly correlated between five of the seven populations (Repparfjordelva, Altaelva, Saltdalselva, Strynselva, and Drammenselva). Also, for the sixth population (Eira), the growth correlated significantly with

Fig. 4. Relationship between mean growth increment for the first year at sea (±2 SE) and median date of smolt migration to sea (day of the year) for (*a*) 1SW fish, (*b*) 2SW fish, and (*c*) 3SW fish, and between daily growth rate for the first year at sea (mm per day ± 2 SE) and latitude for (*d*) 1SW fish, (*e*) 2SW fish, and (*f*) 3SW fish of the seven Atlantic salmon populations. Estimation of daily growth rate is based on the assumption that fish cease growing at the end of December. Regressions: (*a*) $y = -1.01x + 442$, $F_{[1,5]} = 18.9$, $R^2 = 0.791$, $p = 0.007$; (*b*) $y = -1.44x + 529$, $F_{[1,5]} = 71.0$, $R^2 = 0.934$, $p < 0.001$; (*c*) $y = -1.48x + 538$, $F_{[1,5]} = 89.1$, $R^2 = 0.947$, $p = 0.001$; (*d–f*) not significant ($p > 0.05$).

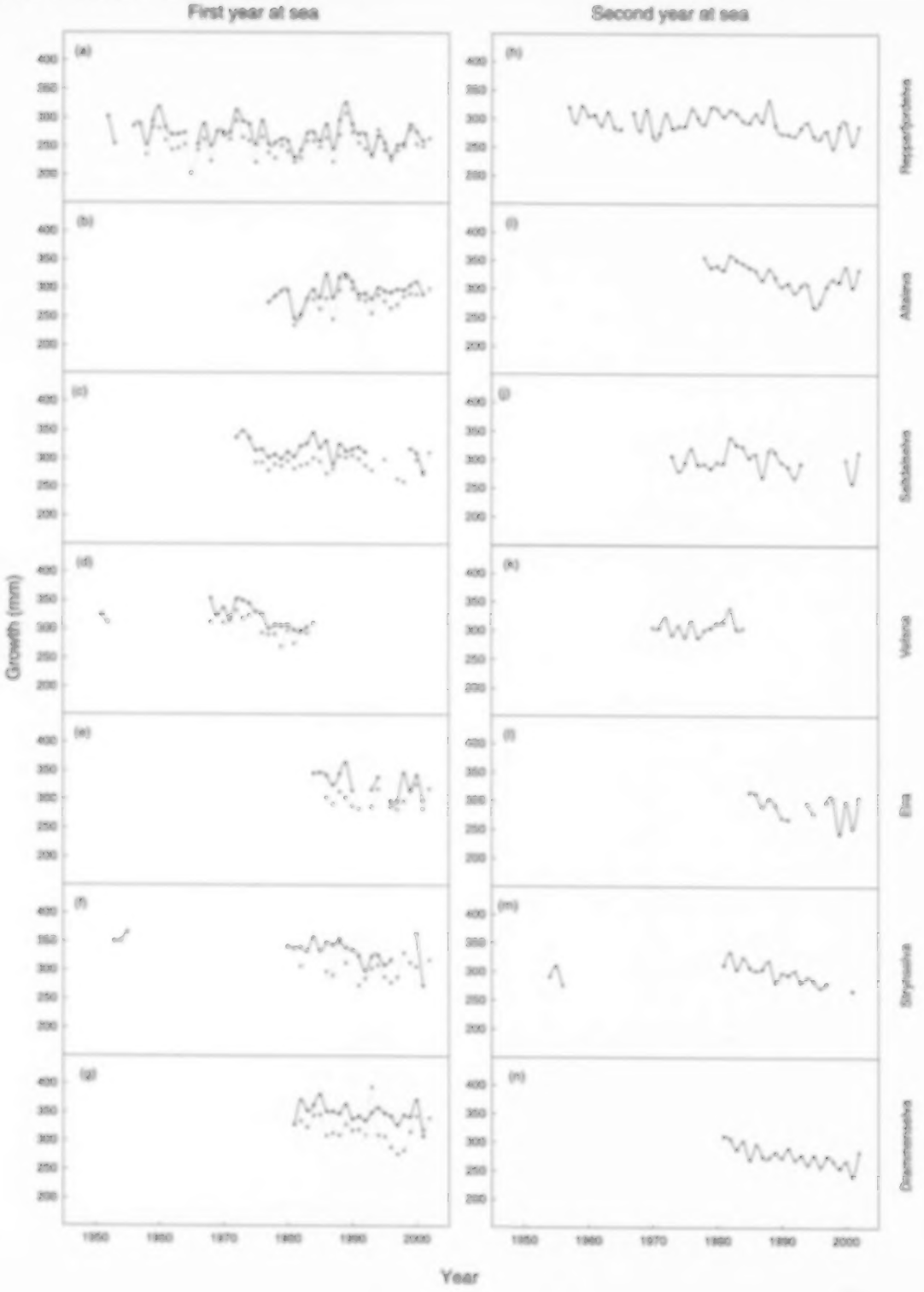


the Altaelva and Saltdalselva populations. The growth increment for the second year at sea of the Vefsna population, however, did not correlate with any of the other populations. In all populations except Vefsna, where growth data were not available after 1984, the growth increment for the second year at sea decreased successively from about 1980 onwards (Figs. 5*h*–5*n*). This decrease in growth with year is partly the reason for the high correlations in growth between these six populations. However, partial correlations, controlling for smolt year, were also significant between the three northernmost populations (Repparfjordelva ~ Altaelva: $r = 0.447$, df = 22, $p = 0.029$; Repparfjordelva ~ Saltdalselva: $r = 0.554$, df = 21, $p = 0.006$; Altaelva ~ Saltdalselva: $r = 0.635$, df = 16, $p = 0.005$). In addition, the mean growth increment of the Eira population was significantly correlated with Altaelva ($r = 0.554$, df = 12, $p = 0.040$) and Saltdalselva ($r = 0.676$, df = 7, $p = 0.046$). When controlling for smolt year, the growth for the second year at sea for the Strynselva and Drammenselva populations did not correlate with any other population ($p > 0.05$).

The time series for growth (Fig. 5) were correlated to pre-fishery abundance data for 1SW fish and 2SW fish retrieved from Friedland et al. (2009*b*). For 1SW salmon, only growth of the Drammenselva population correlated with pre-fishery abundance ($r = 0.536$, $n = 21$, $p = 0.012$). For MSW fish, growth for the first year at sea correlated with pre-fishery abundance in three populations (Drammenselva ($r = 0.596$, $n = 22$, $p = 0.003$), Strynselva ($r = 0.568$, $n = 21$, $p = 0.007$), and Saltdalselva ($r = 0.468$, $n = 27$, $p = 0.014$)). Significant relationships between growth for the second year at sea and pre-fishery abundance were established for the three northernmost populations (Repparfjordelva ($r = 0.408$, $n = 33$, $p = 0.018$), Altaelva ($r = 0.768$, $n = 25$, $p = 0.001$), and Saltdalselva ($r = 0.473$, $n = 24$, $p = 0.020$)), as well as Strynselva ($r = 0.678$, $n = 18$, $p = 0.002$).

Close relationships between sea temperatures and salmon growth were found for populations in the north, but not in the south. For all of the four salmon populations in northern Norway, first year growth was significantly correlated with annual mean SST in the North Sea, the Norwegian Sea, and the Barents Sea (Table 4). However, that of the two most northern populations was most strongly correlated with temperatures at the Barents Sea, whereas growth of the Rivers Saltdalselva and Vefsna salmon showed highest correlation with that in the Norwegian Sea (Table 4). The first year growth increment of salmon from the three southernmost rivers (Eira, Strynselva, and Drammenselva) was not significantly correlated with annual mean SST at any of the three stations (Table 4). For the second year at sea, growth of the

Fig. 5. Time series of growth increment (mm) for the first year (*a*–*g*) and the second year (*h*–*n*) at sea for Atlantic salmon from the seven rivers (1SW, broken lines; MSW, unbroken lines).



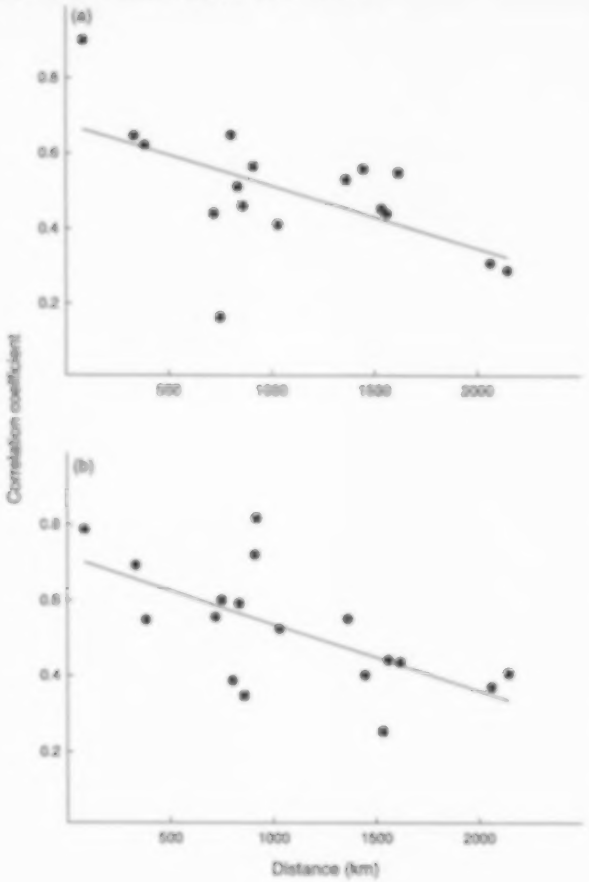


Fig. 6. Pearson's correlation coefficients between growth increment for the first year at sea and distance between the seven populations for (*a*) 1SW salmon and (*b*) MSW salmon.

seven populations was not significantly correlated with temperatures at any of the three stations ($p > 0.05$).

A positive relationship between growth for the first year at sea and SST was also observed on a monthly basis, mainly for the four northernmost populations. Highest correlations were registered for the period May–September, but significant relationships were observed during most of the year. Similar patterns were observed both for 1SW (Fig. 7) and MSW fish (Fig. 8). The growth for the first year at sea also correlated significantly with SST during winter and spring, i.e., several months before the fish entered the sea.

To investigate possible nonlinear relationships between growth and climate indices, we fitted both quadratic and linear regressions for relationships with annual mean SST and for the temperatures in the warmest month (August). None of the regressions showed a significant quadratic term (after sequential Bonferroni correction), so the fit of nonlinear relationships to our data was not investigated further.

Three broad-scale climate forcing indices were tested (the NAO, the AMO, and the subpolar gyre). The subpolar gyre was significantly correlated with both the NAO and AMO indices ($r = -0.539$, $n = 43$, $p < 0.001$; and $r = 0.512$, $n = 43$, $p < 0.001$, respectively), while the NAO and AMO indices were not significantly correlated ($r = -0.143$, $n = 52$, $p = 0.311$). The NAO index increased significantly with time ($r = 0.414$, $n = 52$, $p = 0.002$), while there was no such trend in the other two indices ($p > 0.05$). In general, the first year growth increment was more closely associated with sea temperatures than with these indices. No relationship was found between the subpolar gyre and first year growth, and for only one group (MSW fish from Vefsna), a significant (negative) relationship between the AMO index and first year growth was found ($r = -0.590$, $n = 18$, $p = 0.010$). The NAO index correlated with first year growth in four of the seven populations, all of them located in northern or central Norway (Repparfjordelva MSW: $r = 0.350$, $n = 43$, $p = 0.021$; Altaelva 1SW: $r = 0.543$, $n = 22$, $p = 0.009$; Saltdalselva 1SW: $r = 0.415$, $n = 23$, $p = 0.049$; Saltdalselva MSW: $r = 0.520$, $n = 24$, $p = 0.009$; Eira MSW: $r = 0.542$, $n = 15$, $p = 0.037$).

Discussion

Our observations that growth for the first year at sea of grilse (1SW) in all populations was lower than for larger salmon (MSW) are in accordance with several other studies on Atlantic salmon on both sides of the Atlantic (Gardner 1976; Dempson et al. 1986; Nicieza and Braña 1993). The reasons for this difference in growth rate are not clear, and exceptions exist (Friedland et al. 2009*a*). In the west Atlantic, Saunders (1969) and Anderson (1985) suggested that grilse and MSW salmon have different migration routes at sea. This was supported by Dempson et al. (1986) who rejected the possibility that samples or results were biased, and found strongest evidence for an environmental influence on sea growth rate and age at first maturity. However, our data do not support this hypothesis. Although grilse and MSW salmon might have different migration routes during parts of the first year at sea, it is unlikely that MSW fish from all of our rivers, which are located up to 2000 km apart, have the opportunity to systematically migrate to other and richer feeding areas than 1SW fish rather early in the post-smolt part of their lives, when the main part of post-smolt growth takes place. However, potential grilse and MSW salmon may separate after some time at sea, and may reside in different areas when the winter zone is formed on the scales. Because the pattern of circuli spacing and annulus formation seem to be a response to photoperiod and food availability experienced by the fish at sea (Barber and Walker 1988), this may result in differences in the timing of the formation of the first winter zones among the sea age groups, and hence, cause different growth estimates. Alternatively, evolutionary processes favour larger egg-laying females, and this may be the determining factor controlling growth extent and schedule instead of the area used at sea.

We cannot rule out the possibility that lower growth for the first year at sea of 1SW than MSW fish may be an artifact of our back-calculation method. However, also subsamples analyzed with the Fraser–Lee method gave lowest growth for 1SW fish. Also, if the MSW group contain a number of unidentified previous spawners (Myers and Hutchings 1987), this may lead to a slight overestimation of their back-calculated lengths, because abrasion of the scale

Table 4. Correlation between growth increment for the first year at sea of 1SW and MSW Atlantic salmon from seven Norwegian rivers, and mean annual temperatures at the temperature stations in the Barents Sea (St. 1), Norwegian Sea (St. 2) and North Sea (St. 3) the same year as the fish migrated to sea as smolts.

	Barents Sea		Norwegian Sea		North Sea	
	1SW	MSW	1SW	MSW	1SW	MSW
Repparfjordelva						
r	0.624*	0.660*	0.499*	0.536*	0.425*	0.385*
p	<0.001	<0.001	<0.001	<0.001	0.004	0.008
n	45	46	45	46	45	46
Altaelva						
r	0.685*	0.419	0.553*	0.510*	0.608*	0.321
p	<0.001	0.037	0.008	0.009	0.003	0.117
n	22	25	22	25	22	25
Saltdalselva						
r	0.527*	0.541*	0.543*	0.299	0.538*	0.147
p	0.010	0.008	0.007	0.166	0.008	0.504
n	23	23	23	23	23	23
Vefsna						
r	0.507	0.769*	0.789*	0.806*	0.777*	0.552*
p	0.065	0.001	0.001	<0.001	0.001	0.022
n	14	17	14	17	14	17
Eira						
r	0.310	0.143	0.538*	–0.003	0.173	–0.139
p	0.261	0.597	0.043	0.991	0.537	0.607
n	15	16	15	16	15	16
Strynselva						
r	0.500	0.297	0.371	0.183	0.349	–0.117
p	0.068	0.191	0.192	0.426	0.221	0.612
n	14	21	14	21	14	21
Drammenselva						
r	0.360	0.001	0.076	–0.206	0.092	–0.383
p	0.109	0.998	0.743	0.357	0.692	0.078
n	21	22	21	22	21	22

Note: An asterisk (*) denotes significance after sequential Bonferroni correction with three tests and $\alpha = 0.05$; *r*, Pearson correlation; *p*, level of significance; *n*, number of data sets.

during spawning leads to the scale being smaller for these fish length than for maiden fish.

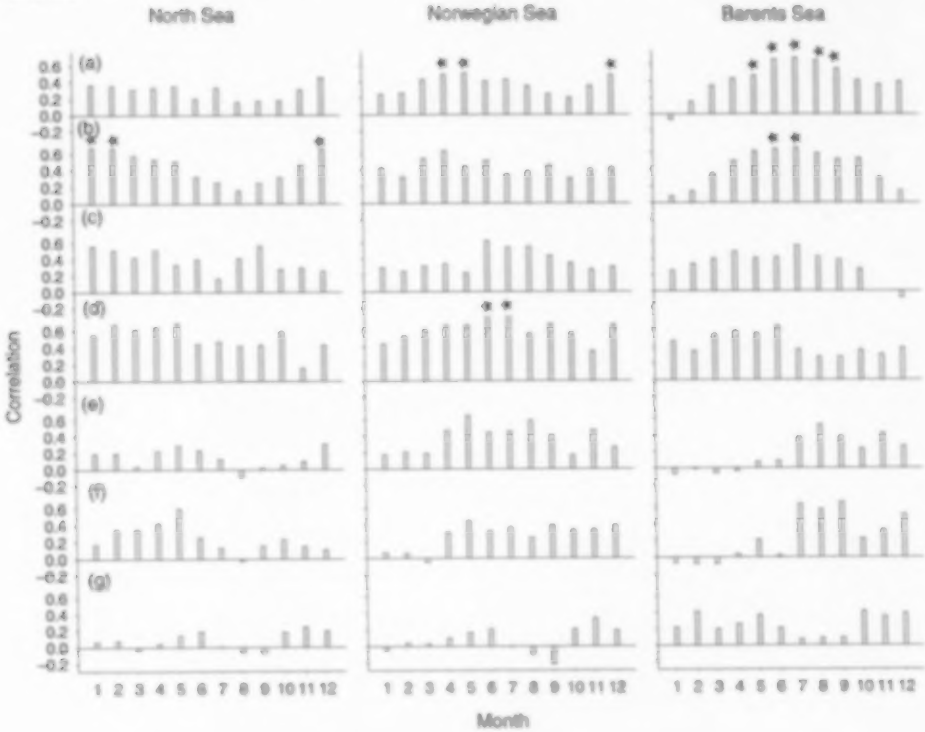
Another reason for the reduced growth in length may be that 1SW fish, which were due to spawn the following autumn, initiated physiological changes to prepare for maturation at the end of their first growth season at sea, including storing lipid reserves at the sacrifice of growth (Thorpe et al. 1998; Mangel and Satterthwaite 2008). According to Mangel and Satterthwaite (2008), the onset of the maturation process starts one year before spawning. Lipid reserves are important for this process, and in those individuals with sufficiently high lipid stores, investment in gonadal tissue will commence. Provided that lipid stores remain sufficiently high throughout the winter, maturation will be maintained (Mangel and Satterthwaite 2008). In the sea, the annulus formation seems to be completed by December or January in anadromous salmonids (Bilton and Ludwig 1966), and hence the switch from growth to storing of lipids takes place before the annulus formation, resulting in reduced growth in length in the post-smolt period compared with immature fish. The lower growth of females compared with males for the first year at sea, indicates that females allocate more energy to lipid storage at this early stage of maturation.

We observed a south–north gradient in growth, with highest growth the first year at sea in the southernmost populations. However, daily growth rates during this period were not significantly different among populations. Along the coast of Norway, smolts enter the sea in early May in the south and as late as late June or early July in the far north (Hvidsten et al. 1998). Hence, the main reason for higher growth for the first year at sea in southern populations is the earlier sea entrance of the fish, where the food conditions are considerably better than in fresh water. However, interannual variability in migration dates over the study period may contribute to the synchronous growth for the first year at sea in nearby populations. Higher sea temperatures in the south may also contribute to higher growth rates, but this also depends on food availability and food quality (Brett et al. 1969). For the second year at sea, the latitudinal trend was the opposite, with highest annual growth rates in northern populations, suggesting that the populations may feed in other areas this time period.

Interannual growth for the first year at sea for Atlantic salmon from rivers that were close to each other was more synchronous than for salmon from distantly separated rivers. Also, first year growth was most strongly correlated with sea temperatures at the stations located closest to the rivers. Smolts from close rivers are expected to enter a more similar marine environment than smolts from more distant rivers, and hence are subjected to more similar temperature and feeding conditions in the early sea phase. The largest marine mortality is believed to take place at the early post-smolt phase (Hvidsten and Møkkelgjerd 1987; Fisher and Pearcy 1988; Hvidsten and Lund 1988). Therefore, ocean climate during this phase is expected to be important for growth and survival (Dannevig 1949; Friedland et al. 1998; Hvidsten et al. 2009). Friedland et al. (2000) and Peyronnet et al. (2007) both found clear indications of a linkage between ocean climate and post-smolt growth and survival of nearby populations of salmon. However, the timing of smolt descent from nearby rivers is similar (Hvidsten et al. 1998), and hence the observed high correlations in first year growth between nearby populations may also be due to a similar length in growth period during the first year at sea.

The distribution, mortality and growth of salmon in the ocean have been found to be related to sea surface temperatures (SST) (Reddin and Shearer 1987; Friedland et al. 2000; Friedland et al. 2009*b*), although other factors like plankton food resources in the post-smolt nursery area are known to be important (Friedland et al. 2009*b*). Faster growth during the post-smolt period results in lower accumulated mortality in a cohort, and hence, higher recruitment (Friedland et al. 2009*b*). The optimum temperature for growth of Atlantic salmon in seawater is not known, although Handeland et al. (2003) estimated it to be about 13 °C from rather sparse data on Norwegian farmed strains of post-smolts, and Smith et al. (2009) obtained a maximum of 14 °C from simulations with a bio energetic model. For juveniles in fresh water it has been estimated to be between 16 °C and 20 °C with food supply in excess, with food con-

Fig. 7. Correlation between monthly mean sea surface temperature (SST) in selected areas of the North Sea, the Norwegian Sea, and the Barents Sea, and growth of 1SW Atlantic salmon for the first year at sea. Monthly SST for the calendar year when smolts entered the sea is given. Panels (*a*) through (*g*) are for the rivers Repparfjordelva, Altaelva, Saltdalselva, Vefsna, Eira, Strynselva, and Drammenselva, respectively. An asterisk (*) denotes significance after sequential Bonferroni correction with 36 tests and $\alpha = 0.05$. The numbers on the *x*-axis refer to calendar months.



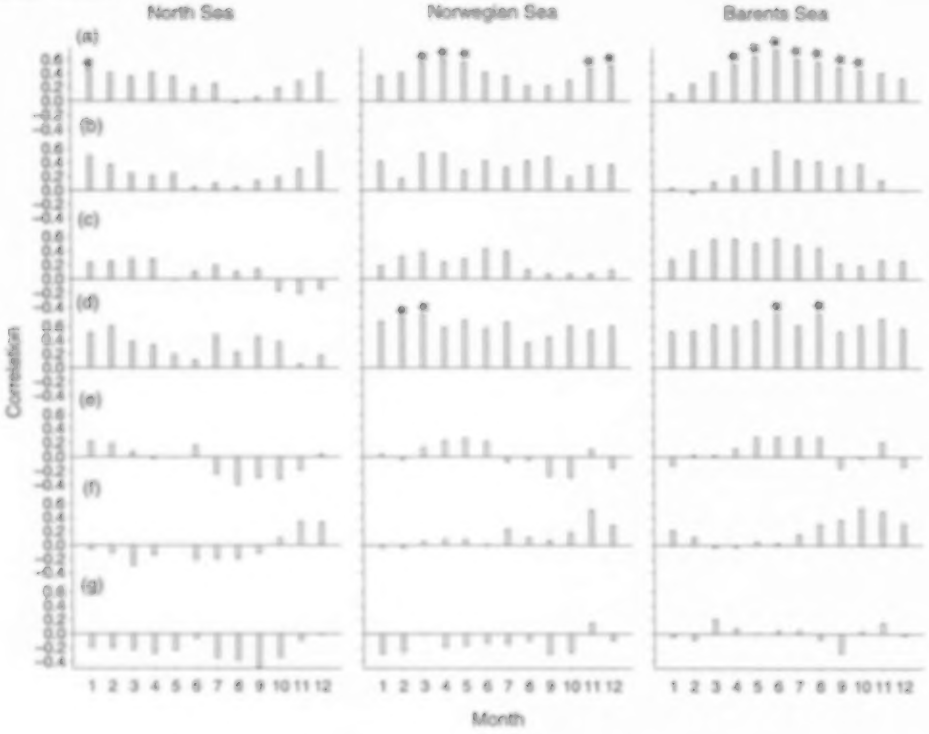
sumption peaking at 19–21 °C (Jonsson et al. 2001). However, the optimum temperature for growth decreases with decreasing food rations (Brett et al. 1969), and experimental data on behavioural thermoregulation by fish generally indicate that the preferred temperature selected by fish seems to be similar to the temperature yielding optimal growth rates (Jobling 1981). Hence, temperature preferences at sea may be considerably lower than that optimal at excess rations (Welch et al. 1995). Most post-smolts caught by floating trawls in the Norwegian Sea during summer (May–August/September) were captured at sea surface temperatures between 8 °C and 11 °C (Holm et al. 2004). In the Baltic Sea, Alm (1958) reported that feeding salmon avoided water temperatures above 11–12 °C. In the same area, Jutila et al. (2005) observed increased survival rates of Atlantic salmon post-smolts when SST in June increased up to 12 °C, and then decreased at higher temperatures.

A temporal and spatial match between increasing SST conditions and reduced growth and survival of post-smolts has recently been demonstrated (McCarthy et al. 2008; Friedland et al. 2009*b*). Friedland et al. (2009*b*) found highest correlations with July and August temperatures, suggesting that warm conditions have a negative influence on growth and recruitment. Their study was conducted mainly on salmon from Scotland and southernmost Norway, indicating that temperatures in areas where these stocks are feeding during the first summer at sea may occasionally be higher than the preferred temperatures. This is in contrast to this study, where first year growth of salmon from northern Norway was highly positively correlated with sea temperatures, but accords well with the lack of correlation between sea temperatures and first year growth in the southernmost populations. Hence, the northernmost populations may, at least in the first part of their sea life, reside in colder sea water and probably further to the north, and hence mainly experience temperatures lower than preferred.

Winter temperatures may also affect salmon growth. Todd et al. (2008) reported a negative relationship between the condition of 1SW Atlantic salmon from a Scottish river and winter (January) SST. However, a similar relationship has not been found for any of six Scottish fisheries over a longer time period (Bacon et al. 2009). We found greatest correlation between growth and SST during summer months. However, in some cases, SST during winter and spring were also correlated with growth, i.e., at a time well before the smolts had left the river. Most cases were for the northernmost populations, and all these correlations were positive. This may indicate that SST is an indicator of other processes (i.e., productivity, prey distribution) so relationships with SST may not solely be the result of temperature effects on the physiology or optimal performance of Atlantic salmon.

Both the high correlations found in marine growth among

Fig. 8. Correlation between monthly mean SST in selected areas of the North Sea, the Norwegian Sea, and the Barents Sea, and growth of MSW Atlantic salmon for the first year at sea. Monthly mean sea surface temperature (SST) for the calendar year when smolts entered the sea is given. Panels (*a*) through (*g*) are for the rivers Repparfjordelva, Altaelva, Saltdalselva, Vefsna, Eira, Strynselva, and Drammenselva, respectively. An asterisk (*) denotes significance after sequential Bonferroni correction with 36 tests and $\alpha = 0.05$. The numbers on the *x*-axis refer to calendar months.



nearby populations and the high correlations found between growth and temperature at the SST area closest to each river, indicate that large parts of the Nordic Seas are used as feeding areas for Atlantic salmon, and suggest that salmon from northern rivers, during both the first and second year at sea, partly stay in other areas than those occupied by southern populations. Results from tagging and recapture experiments confirm that southern and northern populations are partly found in different areas of the Atlantic Ocean (Hansen and Jacobsen 2000; Hansen and Jacobsen 2003; Rikardsen et al. 2008). Furthermore, contrasting growth patterns indicate that populations from the White Sea basin may utilize feeding areas quite distinct from those used by fish that migrate directly into the Barents Sea and Atlantic Ocean (Jensen et al. 1999). In general, post-smolts from distant rivers are necessarily separated for the first period at sea, but after some months they may occur in the same area. Holm et al. (2004) demonstrated that post-smolts from southern Europe had migrated far north in the Norwegian Sea as early as July. Hence, the timing of the smolt migration could be related to the distance each population has to migrate to their feeding areas at sea. However, local climate may also be important for the timing of smolt migration (Hvidsten et al. 1998).

A common negative trend in growth with year was observed both for the first and the second year growth at sea. This was most pronounced for the second year at sea, and after around 1980. Marine growth of salmon has been linked to survival, with higher survival rates at enhanced growth (Friedland et al. 2000; Peyronnet et al. 2007; McCarthy et al. 2008). Data on survival of Atlantic salmon at sea are sparse, and after demonstrating a clear relationship between return rates of the Figgjo and North Esk stocks and pre-fishery abundance of European salmon, Friedland et al. (2009*b*) suggested pre-fishery abundance to be used as a signal for survival. The positive relationship we observed between growth and pre-fishery abundance in most of our populations supports this. However, while the earlier studies documented a relationship between growth and survival for post-smolts only, our study indicates that growth both for the first and the second year at sea may affect survival. In fact, this relationship was most pronounced for growth for the second year at sea.

In this study, the NAO index was more closely related to salmon growth than the AMO index, while no relationship with the subpolar gyre was found. However, post-smolt growth was more closely associated with sea temperatures than with the broad-scale climate-forcing indices. Similar observations were made by Friedland et al. (2009*b*). They documented a relationship between the AMO index and survival of Atlantic salmon in the Norwegian Sea, and found salmon recruitment to be more closely associated with the

AMO than the NAO. However, they concluded that processes related to water temperature are of greater importance to recruitment than atmospheric pressure. Also in North Atlantic seabirds, SSTs tended to explain more of the variability in seabird survival than did the NAO (Durant et al. 2003; Sandvik et al. 2005). Hence, in spite of several advantages with broad-scale climate forcing indices (Stenseth et al. 2003), data on local weather, when available, seem to have the benefit of being more directly linked to mechanisms actually affecting the particular system.

This study demonstrates large variation in the marine growth of Atlantic salmon among populations and years. Growth is closely related to sea temperatures, especially for northern populations, and variations in growth among years correlate significantly between closely situated populations. Also, latitudinal variation in salmon growth during both the first and second year at sea, suggests that northern populations partially occupy different areas than the more southern populations. Several studies on Atlantic salmon show significant relationships between growth and survival (Friedland et al. 2000; Jonsson and Jonsson 2003; Peyronnet et al. 2007), suggesting that post-smolt growth is an indicator of survival. Owing to the problems with estimating the marine survival of salmon, time series of marine growth may provide useful information on the conditions for salmon at sea, and thus be a tool for monitoring salmon populations. The synchronous variation in growth between closely situated populations suggests that this parameter may reflect the general productivity of the whole ecosystem.

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Dynamics of two sailfin sandfish (*Arctoscopus japonicus*) stocks in the Sea of Japan, and their management

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Abstract: The dynamics of the northern and western Sea of Japan sailfin sandfish (*Arctoscopus japonicus*) stocks (NSJ and WSJ, respectively) varied simultaneously until the mid-1970s but differently thereafter. To identify the mechanisms underlying these dynamics, we evaluated the impact of environment and harvesting on NSJ by developing a recruitment model and simulating NSJ dynamics. The model was constructed based on egg production, density effect, and water temperatures in winter and spring, which correlated significantly and positively with the estimated surface mixed-layer depth. Winter water temperatures and egg production were variables common to the two stocks. Our results suggest that simultaneous dynamics resulted from similarities in variations in winter water temperatures for each stock and the difference in dynamics resulted from NSJ depletion caused by overfishing. We suggest management strategies to prevent NSJ depletion caused by unfavorable environmental conditions and overfishing, as well as to allow improved biomass recovery while taking advantage of favorable environmental conditions, and avoid further exploitation of previously depleted NSJ.

Résumé : Les dynamiques des stocks du toroumoque japonais (*Arctoscopus japonicus*) du nord et de l'ouest de la mer du Japon (respectivement NSJ et WSJ) ont varié de concert jusqu'au milieu des années 1970 pour différer par la suite. Afin d'identifier les mécanismes sous-jacents à ces dynamiques, nous avons évalué l'impact de l'environnement et de la récolte sur le stock NSJ en mettant au point un modèle de recrutement et en simulant la dynamique du stock NSJ. Le modèle est construit sur la base de la production d'œufs, de l'effet de la densité, et des températures de l'eau en hiver et au printemps, qui sont en corrélation significative et positive avec la profondeur estimée de la couche de mélange de surface. Les températures de l'eau en hiver et la production d'œufs sont des variables qui s'appliquent aux deux stocks. Nos résultats indiquent que la dynamique simultanée résulte de ressemblances dans les variations dans les températures d'hiver pour les deux stocks et que les différences de dynamique s'expliquent par un déclin du stock NSJ à cause de la surpêche. Nous proposons des stratégies de gestion pour empêcher le déclin du stock NSJ causé par les conditions environnementales défavorables et la surpêche, ainsi que pour permettre une meilleure récupération de la biomasse en profitant des conditions environnementales favorables et pour éviter une exploitation supplémentaire du stock NSJ déjà réduit.

[Traduit par la Rédaction]

Introduction

Understanding fish stock dynamics is important for the prevention of stock depletion and for rebuilding depleted stocks. Several fisheries stocks have already been severely depleted (Pauly et al. 2002), and depletion due to environmental conditions or recruitment overfishing, as well as its prevention, needs to be investigated (Jacobson and MacCall 1995). Thus, impacts of the environment and harvesting on stock dynamics were investigated by developing an intimate dynamics model to determine future management strategies for preventing stock depletion and rebuilding depleted stocks.

We focused on the dynamics of northern and western Sea of Japan sailfin sandfish (*Arctoscopus japonicus*) stocks (NSJ and WSJ, respectively), which are important demersal resources (Fig. 1). The biomass of NSJ (BNSJ) was >30 000 tonnes in 1965–1975 (Watanabe et al. 2005*a*) and was similar to the total catch of WSJ (CWSJ) (Fig. 2), which was the adequate abundance index of WSJ because these catches correlated significantly with the density index as per the offshore fishery (Watanabe et al. 2006). However, since 1980,

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Fig. 1. Summary of locations. The black areas and Station 1 (ST) represent spawning grounds of the northern Sea of Japan sailfin sandfish stock (NSJ) and a point 9 km off Cape Nyudo sampled for water temperature, respectively. The striped area and areas A–G for the 1° grid obtained by Watanabe et al. (2006) indicate the spawning ground of the western Sea of Japan sailfin sandfish stock (WSJ) and areas sampled for water temperature obtained from the Korea Oceanographic Data Center, respectively.

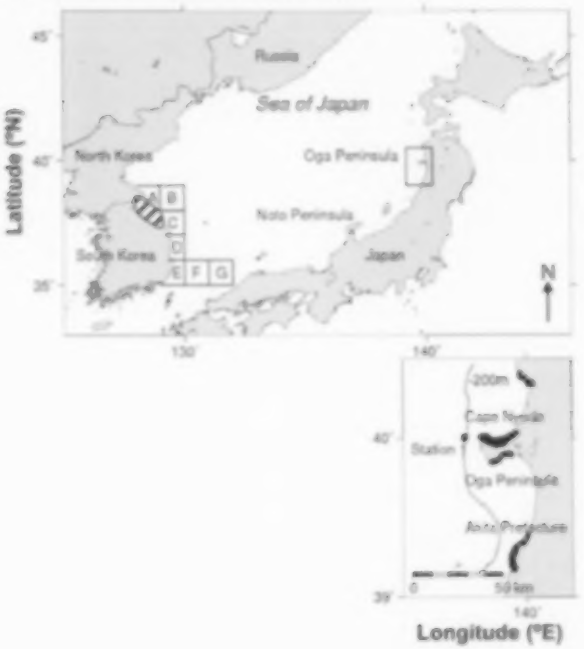
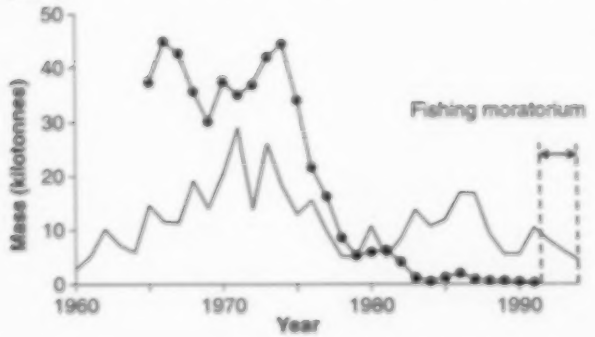


Fig. 2. Biomass of the northern Sea of Japan sailfin sandfish stock (BNSJ) (unbroken line with filled circle) as derived by Watanabe et al. (2005*a*) and total catch of the western Sea of Japan sailfin sandfish stock (CWSJ) (unbroken line) as derived by Watanabe et al. (2006).



BNSJ declined alarmingly to 246 tonnes in 1991, and fishermen in Akita Prefecture eventually introduced a voluntary fishing moratorium in 1992–1994 (Sugiyama 1998). On the other hand, CWSJ had increased during 1980–1988. Simultaneous variation in BNSJ and CWSJ in the 1960s–1970s and subsequent differential variation remain unresolved, because of insufficiently analyzed dynamics of the entire NSJ (Watanabe et al. 2005*b*). We comprehensively investigated the mechanisms underlying the dynamics of the entire NSJ using several approaches.

Fish recruitment within the same region could be synchronized by the widespread variability in ocean environments (Kawasaki 1983; Koslow 1984) and could also be influenced by spawning stock biomass (SSB) and density effects (Ricker 1954). Sakuramoto et al. (1997) suggested that NSJ coastal catch variability was influenced by water temperatures. The potential effects of water temperature, SSB, and density dependence on NSJ recruitment dynamics can be investigated using statistical recruitment models.

Variability in water temperatures could be linked with ecosystem. Chiba et al. (2005) reported that phytoplankton and zooplankton productivities in the Sea of Japan abruptly decreased from the mid- to late-1970s. Primary productivity is generally associated with surface mixed-layer depth (MLD) variability (Polovina et al. 1995). MLD in the Sea of Japan increases during winter–spring (Hirai 1995) corresponding to NSJ life-stages (eggs–juveniles) (Okiyama 1990). CWSJ increased with increasing SSB and winter water temperatures at depths > 150 m in areas D and E in the past, with which MLD correlates positively and significantly (Watanabe et al. 2006) (Fig. 1). We examined the relationships between plausible water temperatures and MLD, and then compared the factors affecting NSJ and WSJ dynamics to ensure the credibility of the calculated potential effects on NSJ recruitment dynamics.

The effects of harvesting were also evaluated by exploitation rates, which reflect the degree of recruitment overfishing, and by simulating NSJ dynamics using the developed recruitment model. We suggest appropriate management based on our results.

Materials and methods

Features of fisheries and life histories of sailfin sandfish stocks in the northern and western Sea of Japan

NSJ and WSJ are distributed mainly in waters from the Oga Peninsula to the Noto Peninsula, and the eastern waters of the Korean Peninsula – Noto Peninsula, respectively (Watanabe et al. 2004; Yanagimoto 2004; Shirai et al. 2006) (Fig. 1). Fisheries for NSJ operate in coastal and offshore waters (Sugiyama 1991). In coastal waters, passive fishing performed using set nets and gillnets harvest spawners, which migrate to spawning grounds around the Oga Peninsula in Akita Prefecture in late November or December. Maturity rates of female fish age >1 year are approximately 100% (Mio 1967). However, the high season of coastal fishing lasts only 1 week in each of the coastal fishing areas. The spawning behavior of sailfin sandfish is similar to that of herring (Fiksen and Slotte 2002). Spawners that escape fishing, deposit egg masses on *Sargassum* spp. in shallow waters. The deposited eggs hatch between February and March, and then NSJ larvae and juveniles remain at water depths of approximately 10 m until April or May (Minami and Tanaka 1985; Okiyama 1990). In offshore fishing grounds at stratum depths of 200–300 m, a Danish seine fishery has actively caught immature and mature fish before spawning throughout the year, except for those months in which fishing is prohibited.

In contrast, fisheries for WSJ operate mainly in the offshore waters of Japan and the Republic of Korea (Choi et al. 1983) (Fig. 1). In Japan, the Danish seine fishery has operated predominantly in the western waters of the Noto Peninsula. In the eastern waters of the Korean Peninsula, Korean Danish seine, trawl, and gillnet fisheries capture WSJ throughout the year. Most of CWSJ consists of catches by the Danish seine and trawl fisheries. WSJ has spawning grounds in the east coast of the Korean Peninsula (Lee et al. 2006). Young fish with body lengths of approximately 8 cm have been found before recruitment in waters around area G at a stratum depth of 0–200 m in January (Yamazaki et al. 1981).

Recruitment and egg production of the sailfin sandfish stock in the northern Sea of Japan

NSJ recruitment and egg production were based on stock size (N_{at}) at age a [1, 2, 3, and 4+ (age group >3 years)] in year t (1965–1991) in January, which were recomputed by a virtual population analysis (VPA) (Pope 1972) that was different from that used by Watanabe et al. (2005*a*). Watanabe et al. (2005*a*) indicated that the fishing mortality at older ages was higher than natural mortality (M) for sailfin sandfish during the studied period, and verified the reliability of these estimates, on the basis of the fact that the estimated biomass had positive linear relationships with independent indices (i.e., the annual density index from the Danish seine fishery and the catch per unit effort from an experimental survey using Danish seine nets). Their VPA assumed that the M is 0.14·year^{-1}, which is an expedient value calculated by Pauly's (1980) method, and the constant fishing mortality at age 4+ (F_{4+t}) is 2.10·year^{-1}, which is given as $Z_{4+} - M$, where Z_{4+} is the conditional total mortality computed by catch at age ($Z_{4+} = 2.24$). However, the constant high F_{4+} assumption may be impractical, and could be worthy of reconsideration, even though it is extremely difficult to investigate the reliability of the estimated M (Hilborn and Walters 1992). No particularly convincing evidence exists suggesting that the behavior of fish at age 4+ is different from that of fish at age 3. In this study, therefore, we recomputed VPA such that F_{4+t} in the most recent year was $(F_{3t} + F_{3t-1} + F_{3t-2})/3$ and F_{4+t} was the same as F_{3t}. However, variation in F_{4+} had little effect on total stock size, because N_{4+t} per total stock size were below 1% in almost all the studied years (Watanabe et al. 2005*a*).

NSJ recruitment (R_t) is given as N_{1t} (individuals), and the egg production (S_{t-2}) that induces R_t is actually spawned in late November or December of year t–2 by escaped mature females (Mio 1967). Therefore, S_{t-2} is defined as

$$(1) \qquad S_{t-2} = \sum_{a=2}^{4+} [N_{at-2} \exp(-M)(1 - E_{at-2}) \times r\psi_{at}]$$

where r is the proportion of females among the total number of fish ($r = 0.5$) given by Kato and Ohuchi (1956), E_{at} is the exploitation rate at age, and ϕ_a is fecundity at age estimated from fecundity – body length regression, as reported by Sugiyama (1988). The indices ϕ_2, ϕ_3, and ϕ_{4+} are 1451, 1916, and 2482 eggs·year^{-1}, respectively.

Ocean environmental data

The following ocean environmental data were used: (*i*) water temperature at Station 1 (ST), which is located 9 km off Cape Nyudo (Fig. 1), at stratum depths of 0–50, 75–150, and 200–300 m in March–December during 1961–1998 (Akita Prefecture 1998); (*ii*) water temperature at areas A–G for each 1° grid at stratum depths of 0–50, 100, 150, 200, and 300 m in February, April, June, August, October, and December during 1960–1999, which were processed from the raw data obtained from the Korea Oceanographic Data Center (2000) (see Fig. 1); and (*iii*) MLD at ST in March–December during 1961–1998. In this study, MLD was calculated as the depth between the sea surface and a stratum of water such that the difference in water temperature between these 2 strata was greater than 1 °C (Kim and Isoda 1998). MLD values were discrete values, because stratum depths at ST are discrete data, such as 0 and 50 m. Hereinafter, T_{idmt} denotes the water temperature in area i (ST, A–G) at stratum depth d, in the month m, of year t, and MLD_{STmt} denotes to MLD at ST in m of t. T_{idmt} at ST was used to derive an environmental variable to incorporate into the R_t models.

Data analysis

We investigated the mechanism underlying NSJ dynamics using the following procedures: (*i*) calculating correlations between R_t dynamics and water temperature at ST; (*ii*) modeling R_t; (*iii*) computing correlations between water temperature at ST at each stratum depth and MLD, when the optimal R_t model incorporated the environmental variable of water temperature; (*iv*) contrasting water temperatures associated with NSJ and WSJ dynamics when the optimal R_t model used the environmental variables; (*v*) comparing variables used in the optimal R_t model with different exploitation rates; and (*vi*) evaluating the impact of harvesting on NSJ dynamics using simulations based on an age-structured dynamic model.

Correlations between recruitment and water temperature

To derive the environmental variable to incorporate into the R_t models, we explored significant correlations between T_{STdmt} at ST and R_t or the natural logarithm of R_t ($\log R_t$). This correlation analysis used T_{STdmt} at 14 months from the spawned egg to age 1 year (i.e., November of t–2 to December of t–1). T_{STdmt} in t without a time lag may affect stock size estimates and catch variability in NSJ through the scalable NSJ distribution, availability of NSJ, and varied M in t (Jacobson and MacCall 1995). However, the coastal and offshore fishing grounds of NSJ were not greatly changed from the 1960s to 1990s (Sugiyama 1991; Watanabe et al. 2004). NSJ coastal catch in t are accurately predicted by water temperatures in the past 1–3 years and not by those in t (Sakuramoto et al. 1997). We therefore ignored T_{STdmt} in t in this correlation analysis. We standardized each significant T_{STdmt}, and used the arithmetic mean of these T_{STdmt} values as an environmental variable.

Recruitment models

Different R_t models were constructed for the following cases:

(2) Model 1: $R_t = \alpha \times S_{t-2} + \varepsilon_t$

(3) Model 2: $R_t = \alpha \times S_{t-2} \times U_{t-2} + \varepsilon_t$,
$U_{t-2} = \exp(-\beta \times S_{t-2})$

(4) Model 3: $R_t = S_{t-2} \times W_{t-1} + \varepsilon_t$,
$W_{t-1} = \exp[-(\alpha_0 + \alpha_1 \times \mathrm{ENV}_{t-1})]$

(5) Model 4: $R_t = S_{t-2} \times W_{t-1} \times U_{t-2} + \varepsilon_t$, where α, α_0, α_1, and β are the parameters of these equations, and ε_t is the error term that is normally distributed, with mean 0 and variance σ^2. Model 2 represents Ricker's (1954) curve, and U_{t-2} is the density-dependent survival rate. Model 3 indicates that R_t depends on both S_{t-2} and the environmental survival rate (W_{t-1}), which is the exponentially related to the environmental variable (ENV_{t-1}) of $T_{\mathrm{ST},dmr}$. To estimate the parameters, a maximum likelihood method was used and an optimization was run using a quasi-Newton method and the Solver algorithm in Microsoft Office Excel® (Microsoft Corporation 2003). We selected an optimal model by comparing the performance of each model on the basis of finite correction using the Akaike information criterion for small samples ($\mathrm{AIC_c}$; Sugiura 1978) and a likelihood ratio test. The normality of standardized residuals was calculated using the Jarque–Bera test (Bowman and Shenton 1975).

Correlations between water temperature and surface mixed-layer depth

To clarify the relationships between $T_{\mathrm{ST},dmr}$ and ocean events, we computed correlation coefficients between $\mathrm{MLD}_{\mathrm{ST},mr}$ and $T_{\mathrm{ST},dmr}$ at each stratum depth for each month in which R_t or log R_t correlated positively and significantly with $T_{\mathrm{ST},dmr}$.

Comparing water temperatures associated with different stock dynamics

Water temperatures incorporated into the optimal R_t model were compared with $T_{\mathrm{D150Dec},t}$ and $T_{\mathrm{D200Dec},t}$ at area D, and $T_{\mathrm{E150Dec},t}$ at area E in December (see Fig. 1), which were the key factors in WSJ dynamics (Watanabe et al. 2006).

Comparing variables used in the optimal model with exploitation rates

To clarify the impact of variables incorporated into the optimal R_t model and harvesting on NSJ dynamics, we compared the trajectories of incorporated variables with those of different exploitation rates. We calculated the total exploitation rate (E_t) as

$$(6) \qquad E_t = \sum_{a=1}^{4+}[C_{at}\exp(M)] \cdot [\sum_{a=1}^{4+} N_{at}]^{-1}$$

where C_{at} is the catch at age derived by Watanabe et al. (2005*a*). Using the same procedure as described in eq. 6, exploitation rates at age (E_{at}), at the coastal (ECOAST_t), and offshore fisheries (EOFF_t) were also calculated with C_{at}, an age-combined catches from the coastal and offshore fisheries, respectively.

Simulations

As mentioned above, from 1976 to 1979, BNSJ decreased dramatically with CWSJ, and was then remained at an extremely low level for >10 years, whereas CWSJ increased again from 1980 (Fig. 2). To evaluate the effects of harvesting during the mid-1970s to 1980s on NSJ dynamics, we simulated NSJ dynamics under various assumptions as described in Table 1. The first goal of the simulation was to investigate the impact of harvesting under the constant W_{t-1} on NSJ dynamics, when the optimal R_t model incorporated W_{t-1}. Therefore, we made assumptions 1–3, in which W_{t-1} during 1976 to 1991 was a mean value from 1966 to 1975. The second goal was to investigate the impact of the timing of fishery closure for 1 year on NSJ dynamics. Therefore, we made assumptions 4–6, in which the fisheries were only closed in 1978, 1979, and 1980, respectively. Third, to determine the effects of a reduction in the assumed exploitation rate at age (E'_{ak}) for 5 years (1978–1982) instead of a prohibition on fishing, we made assumptions 7 and 8 because, in practice, it is extremely difficult to achieve complete fisheries closure. Finally, to assess the effects of a reduction in E'_{ak} on NSJ dynamics after BNSJ was already depleted, we made assumptions 9 and 10, in which E'_{ak} was reduced in 1983–1987. We set the regulated period to 5 years, because this period covered from k to k +4, until R_{k+2} (i.e., N_{1k+2}) affected by E'_{ak} becomes N_{3k+4}. This period does not allow for N_{4+k+5} in year k +5, because the actual N_{4+t} values at terminal age were always less than 5% of the total stock size in t.

In this study, a deterministic age-structured dynamic model, which is appropriate for understanding the basic principles of stock dynamics, was considered to simulate NSJ dynamics:

$$(7) \qquad \mathrm{BNSJ}_{k+1} = [(R_{k+1})(\chi_1)] + \sum_{a=2}^{4+}\{[N_{a-1k}\exp(-M)] \times (1 - E'_{a-1k})\chi_a\}$$

where BNSJ_{k+1} is the simulated biomass at the beginning of the year (i.e., January), k is the year in which fishing was regulated, χ_a is body mass at age a in January, and χ_{1-4+} is given separately as 32, 66, 97, and 145 g (Sugiyama 1988), and E'_{ak} is the assumed exploitation rate at age in this simulation (Table 1). The assumed E'_{ak} affects R_{k+2} through S_k harvest, with an interval of 2 years. Therefore, after k +2, NSJ recruitment in eq. 7 is predicted by substituting the calculated S_k into the selected R_t model and only R_{k+1} can be given as the actual recruitment. We then calculated cumulative biomass and cumulative catch from 1978 to 1991 (14 years) and biomass in the last year (1991) under each assumption to evaluate the performances of management by harvesting regulations. We ignored a period of 1975 to 1977 during the simulation under assumptions 1–3 in the evaluation of performances because of unified evaluation for all the assumptions. The simulated total catch (Y'_k) is calculated as

$$(8) \qquad Y'_k = \sum_{a=1}^{4+}\{E'_{ak} \times [N_{ak}\exp(-M)]\omega_a\}$$

where ω_a is body mass at age a in December, and ω_{1-4+} is given separately as 51, 86, 123, and 174 g (Sugiyama 1988).

Table 1. Assumptions for simulations that exploitation rates at age (E'_{ak}) are regulated.

	Script			
Assumption	Regulated period	Regulated E'_{ak}	Postregulated E'_{ak}	Environmental survival rate (W_k)
1	1975–1991	E_{ak}	—	Mean W_k (1966–1975)
2	1975–1991	Mean E_{ak} (1965–1974)	—	Mean W_k (1966–1975)
3	1975–1991	Mean E_{ak} (1975–1991)	—	Mean W_k (1966–1975)
4	1978	0.0	E_{ak}	W_k
5	1979	0.0	E_{ak}	W_k
6	1980	0.0	E_{ak}	W_k
7	1978–1982	$0.8\times E_{ak}$	E_{ak}	W_k
8	1978–1982	$0.7\times E_{ak}$	E_{ak}	W_k
9	1983–1987	$0.8\times E_{ak}$	E_{ak}	W_k
10	1983–1987	$0.7\times E_{ak}$	E_{ak}	W_k

Note: E'_{ak} and E_{ak} denote exploitation rate at age a in year k obtained by simulations and actual exploitation rate, respectively.

Results

Correlations between recruitment and water temperature

R_t correlated positively and significantly with $T_{ST,dmt}$ at 75–150 m in November of t–2, at 200–300 m in April, August, September, and December of t–1, and at 75–150 m in August and November of t–1 (7 $T_{ST,dmt}$). On the other hand, log R_t correlated positively and significantly with $T_{ST,dmt}$ at 200–300 m in April, August, and September of t–1 and at 75–150 m in October and November of t–1 (5 $T_{ST,dmt}$). A total of eight significant $T_{ST,dmt}$ values was observed because there were duplicate $T_{ST,dmt}$ values for 4 of 12 $T_{ST,dmt}$. These eight $T_{ST,dmt}$ appeared during all seasons from egg to age 1. In these eight $T_{ST,dmt}$, only $T_{ST75\text{-}150Aug,t\text{-}1}$ was not available for 1985 and 1988. Consequently, ENV_{t-1} was obtained as the arithmetic mean of 7 $T_{ST,dmt}$ barring $T_{ST75\text{-}150Aug,t\text{-}1}$.

Performance of recruitment models

Of all cases examined, Model 4 had the lowest AIC_c and included S_{t-1}, U_{t-2}, and W_{t-1} constructed by ENV_{t-1} (Table 2). All parameters except β in Model 2 were significant as per the likelihood ratio test (Table 2). Model 4 provided a good explanation of the observed R_t, even though it underestimated R_t in both 1969 and 1970 and, in contrast, overestimated R_t during 1976–1979 (Fig. 3). The frequency distribution of standardized residuals in Model 4 was approximately and significantly normal ($\chi^2 = 8.8$, df = 2, $P < 0.02$). Therefore, the optimal R_t model proved to be Model 4.

Correlation between water temperature and surface mixed-layer depth

In all months except September, $T_{ST,dmt}$ at depths greater than 75–150 m, which also included the significant $T_{ST,dmt}$ configuring ENV_{t-1}, correlated positively and significantly with $MLD_{ST,mt}$ (Fig. 4).

Comparing water temperatures associated with different stock dynamics

Variables common to both NSJ and WSJ dynamics included water temperatures at $d > 75$–150 m in winter, which positively affected both dynamics as well as S_{t-2} (Model 4 in Table 2). Trajectories of $T_{ST75\text{-}150Nov,t}$ (range, 11.3–17.5 °C; mean, 14.8 °C) and $T_{ST200\text{-}300Dec,t}$ (range, 0.9–13.3 °C; mean, 4.8 °C) configuring ENV_t, $T_{D150Dec,t}$ (range, 1.9–11.9 °C; mean, 5.1 °C), $T_{D300Dec,t}$ (range, 1.0–8.2 °C; mean, 2.9 °C), and $T_{E150Dec,t}$ (range, 1.0–15.7 °C; mean, 7.5 °C), associated with WSJ dynamics are shown (Fig. 5). $T_{ST75\text{-}150Nov,t}$ on the eastern sides of the Sea of Japan (Fig. 5*a*) correlated positively and significantly with $T_{TE150Dec,t}$ on the western sides of the Sea of Japan (Fig. 5*c*) ($r = 0.40$, $P < 0.02$). Long-term trends in these five temperatures increased from the 1960s to mid-1970s relative to their respective means, but decreased from the mid-1970s to 1990s relative to their means. However, $T_{ST75\text{-}150Nov,t}$ increased gradually from 1978 to 1981 (Fig. 5*a*). More specifically, $T_{ST75\text{-}150Nov,t}$ exceeded the mean in 1980 and 1981, whereas $T_{D150Dec,t}$ was close to the mean in 1980, but exceeded the mean in 1981 (Fig. 5*b*).

Comparing variables used in the optimal model and exploitation rates

A trajectory of W_{t-1} (range, 0.6%–3.7%; mean, 1.5%) in Model 4 decreased greatly and gradually during the mid-1970s to the 1980s within approximately 10 years (Fig. 6*a*). Remarkably, these values were close to the mean in 1981, but were greater than the mean in 1982, because of the increase in water temperature shown (Fig. 5*a*).

A trajectory of U_{t-2} (range, 18.8%–99.0%; mean, 66.2%) in Model 4 was the inverse of that of S_{t-2} throughout the period studied (Fig. 6*b*). Since 1980, S_{t-2} (range, 5–830 × 10^8 eggs; mean, 276 × 10^8 eggs) was always less than its mean thereafter. Following the decrease in W_{t-1}, S_{t-2} decreased sharply with a time lag of a few years and was the lowest in 1986, with a value of 0.6% of the maximum value.

In contrast, prior to 1979, total E_{t-2} (range, 33.3%–85.7%; mean, 54.9%) was constant, and was less than its mean for 10 of 13 years, whereas $EOFF_{t-2}$ was always less than $ECOAST_{t-2}$ (Fig. 6*c*). However, after 1980, E_{t-2} was greater than the mean for 8 of 12 years, whereas almost all $EOFF_{t-2}$ values were greater than $ECOAST_{t-2}$ values, with increases in E_{1t-2} at age 1 and E_{2t-2} at age 2 (Fig. 6*d*).

Simulations

The actual exploitation rate did not decrease $BNSJ_t$ from the mid-1970s under the constant W_{t-1} (assumption 1) (Fig 7). $BNSJ_t$ under assumption 1 slightly decreased from 1980 to 1983, and then sharply declined after 1986 with an increase in $EOFF_{t-2}$ (Fig. 6*c*). On the other hand, $BNSJ_t$ under assumptions 2 and 3 were gradually converged on approxi-

Table 2. A summary of the recruitment (R_t) model of the northern Sea of Japan sailfin sandfish stock (NSJ).

	Parameter						
Model	α or α_0	α_1	β	AIC_c	$\Delta AICc$	LL	r^2
1	0.005, $P<0.01$			1062	18	−525.80	0.43
2	4.555, $P<0.01$		1.081×10^{-11}, $P = 0.14$	1065	20	−524.71	0.45
3	5.600, $P<0.01$	−0.634, $P<0.01$		1060	16	−522.46	0.58
4	4.375, $P<0.01$	−0.915, $P<0.01$	2.016×10^{-11}, $P<0.01$	1044	0	−512.17	0.79

Note: α, α_0, α_1, and β are the parameters; P value is given by likelihood ratio test; $\Delta AICc$ value is a difference between AIC_c at each model and the lowest AICc; and LL is log-likelihood.

Fig. 3. Recruitments observed (filled circle) and reproduced (open circle) by Model 4.

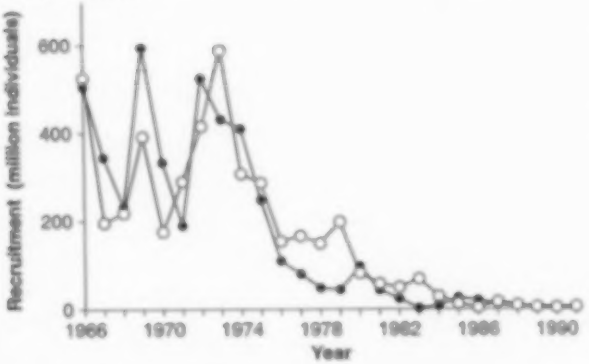


Fig. 4. Correlation coefficients between water temperatures and estimated surface mixed-layer depth at Station 1 at each stratum depth in April, August, September, October, November, and December.

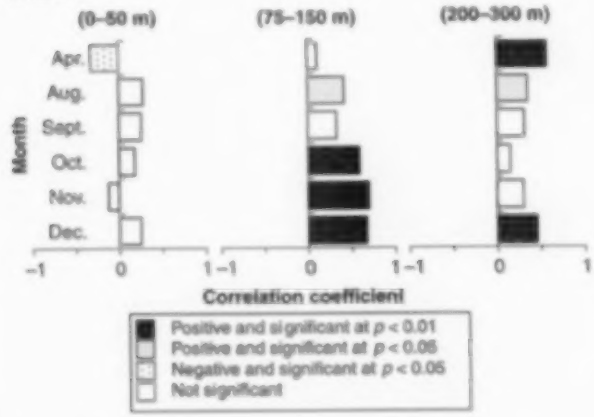
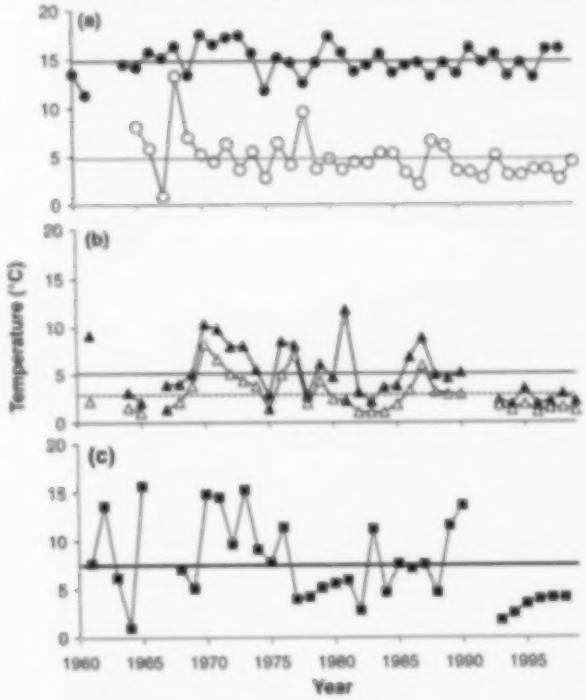


Fig. 5. (*a*) Water temperature at Station 1 at a stratum depth of 75–150 m in November (unbroken line with filled circle) and its mean (unbroken line), and that at a stratum depth of 200–300 m in December (unbroken line with open circle) and its mean (broken line); (*b*) water temperature at area D at a stratum depth of 150 m in December (unbroken line with filled triangle) and its mean (unbroken line), and that at area D at a stratum depth of 200 m in December (unbroken line with open triangle) and its mean (broken line); (*c*) water temperature at area E at a stratum depth of 150 m in December (unbroken line with filled square) and its mean (unbroken line).



mately 37 000 and 32 000 tonnes, respectively. Fishery closure for only one year under assumptions 5 and 6 (Table 1) rapidly increased $BNSJ_t$ when W_{t-1} was close to, or higher than the mean (Fig. 8*a*). Under the assumptions 7 and 8, that E'_{ak} was reduced from 1978 to 1982, $BNSJ_t$ increased efficiently from 1980 with increasing CWSJ (Fig. 8*b*). Cumulative biomass and catch from 1978 to 1991 observed under assumptions 7 and 8 were greater than those observed under assumptions 4, 5, and 6 (Table 3). When S_{t-2} and W_{t-1} were already markedly decreased (Fig. 6), $BNSJ_t$ observed under assumptions 9 and 10 did not increase markedly (Fig. 8*c*). Ratios of calculated cumulative biomass and catch under assumptions 9 and 10 to the actual values ranged from 1.5 to 1.8 and from 1.4 to 1.6, respectively, and were less

Fig. 6. (*a*) Environmental survival rate (W_{t-1}) (unbroken line with filled circle) and its mean (broken line); (*b*) density-dependent survival rate (U_{t-2}) (unbroken line with open circle) and its mean (dotted line), egg production (S_{t-2}) (unbroken line with filled triangle) and its mean (dashed line); (*c*) total exploitation rate (E_{t-2}) (unbroken line with filled circle) and its mean (broken line), and exploitation rates from the coastal fishery ($ECOAST_{t-2}$) (unbroken line with filled triangle) and offshore fishery ($EOFF_{t-2}$) (unbroken line with open circle); (*d*) exploitation rates at ages 1 (open circle), 2 (open triangle), and 3 (filled square) in *t*–2.

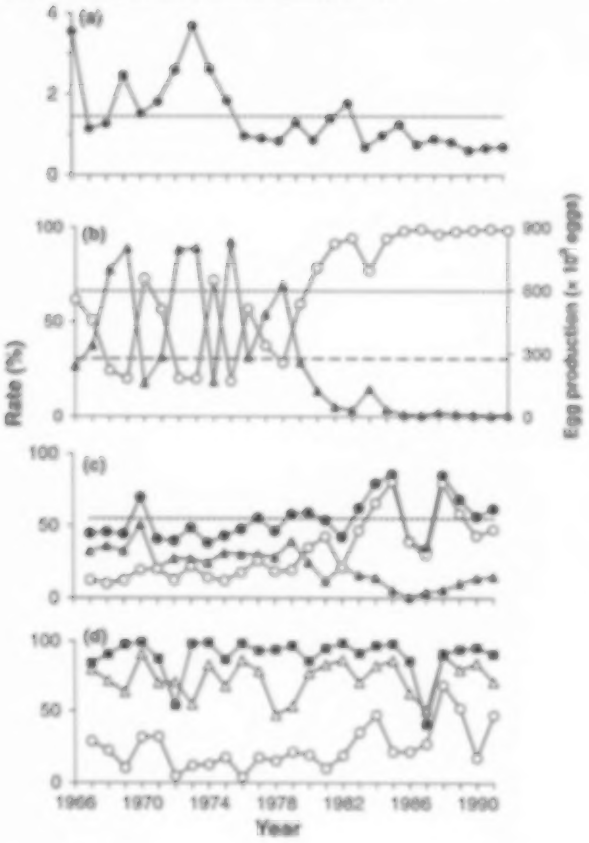
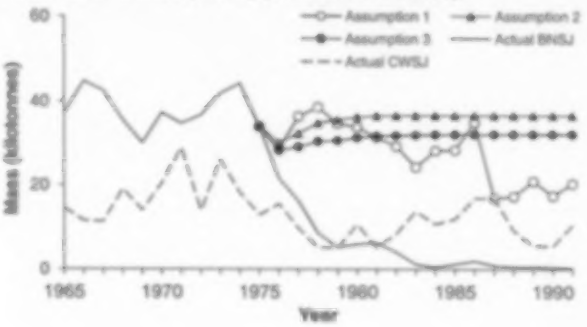


Fig. 7. Biomass of the northern Sea of Japan sailfin sandfish stock ($BNSJ_t$) simulated under assumptions 1–3, the actual biomass of NSJ (BNSJ), and the actual total catch of the western Sea of Japan sailfin sandfish stock (CWSJ) (Watanabe et al. 2006).



than those obtained under other assumptions (Table 3). Ratios of $BNSJ_t$ in the last year under assumptions 1–10 to the actual values ranged from 5.3 to 141.8.

Discussion

Possible mechanisms for recruitment dynamics of the sailfin sandfish stock in the northern Sea of Japan

The optimal recruitment model (model 4) was developed based on egg production, density-dependent survival rate, and environmental survival rate including the water temperature at depths greater than 75–150 m from spawning of eggs to recruitment (egg–recruitment). Variability in water temperature at ST, at depths greater than 75–150 m in winter and spring, correlated positively with variability in MLD, which was markedly enhanced during winter–spring (Hirai 1995; Kim and Isoda 1998). Our results suggest that water temperatures used in the environmental variable are not just plausible, but are important elements in understanding the mechanisms underlying NSJ recruitment dynamics.

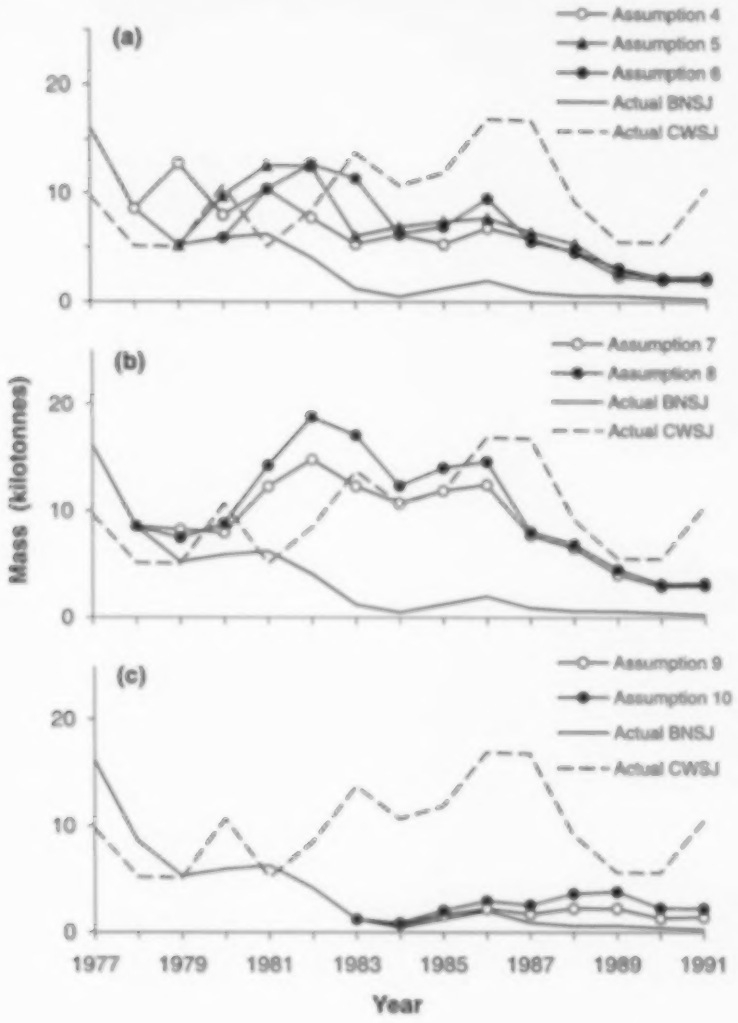
Remarkably, water temperatures in winter, which correlated with MLD, were variables common to both NSJ and WSJ dynamics as well as egg production (or SSB) (Watanabe et al. 2006). Although ST is relatively remote from the eastern waters of the Korean Peninsula, the long-term trends in winter water temperatures responsible for NSJ and WSJ dynamics were similar to each other. In the Sea of Japan, the biomass of phytoplankton and zooplankton reduced markedly from the mid- to late-1970s (Hirota and Hasegawa 1999; Chiba et al. 2005). In conclusion, although the ecological relationship between survival during egg–recruitment and MLD have not been demonstrated, we provide a possible mechanism whereby NSJ recruitment is affected mainly by egg production and winter environmental conditions, which correlates with MLD; this mechanism is similar to that applicable to WSJ dynamics.

In Model 4, the density-dependent survival rate was a factor affecting recruitment dynamics. Fiksen and Slotte (2002) reported that density dependence on the recruitment success of the Norwegian spring spawning herring, which has a spawning behavior similar to that of sailfin sandfish, could be related to a limited number of suitable spawning areas. In fact, in the 1960s and 1970s, when egg production in NSJ was maintained at a high level, many dead egg masses, which were not fixed to the spawning ground by gulfweed, were observed on the sand near the spawning grounds (H. Sugiyama, personal observations). Unfortunately, no data is available to indicate whether density dependence caused this ecological event.

Why did these stock dynamics vary in parallel prior to 1980, and then differently thereafter?

As mentioned above, our results suggest that NSJ and WSJ dynamics were synchronized prior to the mid-1970s because of the similarity in winter environmental conditions for the 2 stocks, and that NSJ and WSJ sharply decreased in parallel after the mid-1970s because of existence of unfavorable environmental conditions for both stocks and not because of recruitment overfishing (assumptions 1–3).

Fig. 8. Biomass of the northern Sea of Japan sailfin sandfish stock ($BNSJ_t$) simulated under assumptions (*a*) 4–6, (*b*) 7 and 8, and (*c*) 9 and 10; the actual biomass of NSJ (BNSJ) and the actual total catch of the western Sea of Japan sailfin sandfish stock (CWSJ) derived by Watanabe et al. (2006).



However, NSJ dynamics have obviously differed from WSJ dynamics since 1980. In the 1970s and 1980s, the environmental survival rate declined gradually. However, during this transition, the environmental survival rate was favorable in 1981 and 1982. Nevertheless, after 1976, the total exploitation rate increased gradually, with intense exploitation rates at age 1 and 2 years, which was primarily caused by offshore fishing. Importantly, our simulation showed that the biomass increased steadily and continuously from 1980, with an increase in the total catch for WSJ when the exploitation rate at age was reduced by 20% and 30%. Therefore, our results suggest that offshore fisheries were responsible for overfishing, especially of fish aged 1 and 2 years, which constitute the potential and present SSB, respectively. Consequently, these fisheries may have destroyed the few possibilities that the biomass had for stock replenishment after 1980 (Watanabe et al. 2005*b*).

During the 1980s and 1990s, both biomass and egg production were extremely reduced. The environmental conditions were also continuously unfavorable for reproduction of NSJ, and harvesting removed a large part of what remained of a small biomass. This harvesting in the 1980s decreased the biomass under the relatively high environmental survival rate (assumption 1). Mizuguchi and Shibata (1992) and Watanabe et al. (2005*b*) pointed out that the NSJ catch number considerably declined after the 1980s, and they also stated that overharvesting may have been a factor in this reduced catch number. Therefore, our results and those of these previous studies imply that exploitation rates during the 1970s and 1980s prolonged biomass depletion, and that high exploitation rates caused severe depletion after the 1980s, even though environmental conditions were continuously unfavorable.

Table 3. Performances of management simulated at each assumption (Table 2) and actual performances.

	Management performance		
Assumption	Cumulative biomass	Cumulative catch	Biomass in the last year (1991)
1	376.8 (13.0)	276.5 (11.7)	20.3 (78.5)
2	510.7 (17.6)	341.8 (14.4)	36.7 (141.8)
3	445.2 (15.4)	317.7 (13.4)	32.2 (124.2)
4	87.6 (3.0)	60.4 (2.5)	2.0 (7.7)
5	95.7 (3.3)	68.7 (2.9)	2.3 (9.0)
6	94.6 (3.3)	69.6 (2.9)	2.3 (8.8)
7	123.4 (4.3)	85.9 (3.6)	3.0 (11.5)
8	141.7 (4.9)	95.1 (4.0)	3.2 (12.4)
9	44.3 (1.5)	34.0 (1.4)	1.4 (5.3)
10	51.0 (1.8)	38.1 (1.6)	2.2 (8.4)
Actual value	28.9	23.7	0.3

Note: The values given in parentheses show the ratios of simulated values to actual values.

Management implications

Understanding of the nature of stock dynamics is of great value in developing management strategies. Our simulation identified the stock-specific nature of NSJ dynamics, wherein harvesting regulations that respond promptly to favorable environmental conditions set-up good management practices, and such regulations prevent prolonged depletion. Walters and Parma (1996) and MacCall (2002) investigated the optimal harvesting strategies under several scenarios, with respect to varied environmental conditions and life histories of different species. Their studies demonstrated that harvesting strategies that respond to environmental conditions achieve superior management-related performance in relatively short-lived populations (herring) (Walters and Parma 1996) and in the Pacific sardine (MacCall 2002), compared with constant harvesting strategies. Therefore, management of NSJ, which supports relatively short-lived species, requires the formulation of a strategy that considers not only the varied biomass (Tanaka 1982; Hilborn 2002) but also the nature of NSJ dynamics associated with environmental variability. However, the problem is that suitable management strategies aim to control the period during which harvesting should be regulated.

Variations in environmental conditions need to be considered while determining the period for harvesting regulations. This problem might include forecasting of these conditions prior to regulation. However, our results show that environmental conditions did not shift sharply from favorable to unfavorable within a single year, but changed gradually over several years; although conditions were deteriorating, reduction of the exploitation rate increased efficiently the biomass by maximizing opportunities for stock recovery (assumptions 7 and 8). Therefore, it is desirable that the period for regulated harvesting could be determined by identifying changes in environmental conditions as soon as possible, once these changes are anticipated or coming. However, patterns of variation in conditions, and correlations between environmental conditions and recruitment dynamics, must be monitored continuously (Myers 1998).

In 1992–1994, to rehabilitate the depleted BNSJ, the fishermen of Akita Prefecture in the NSJ fisheries self-imposed a fishing moratorium (Sugiyama 1998). Sakuramoto et al. (2001) stated that the 3-year fishing closure off Akita Prefecture appeared to be related to NSJ catch recovery in Akita Prefecture, based on a simulation using the NSJ coastal catch model, although environmental conditions were unfavorable during the fishing moratorium. Our simulation indicated that the biomass in 1991 prior to the fishing moratorium was at least 5× the actual biomass in 1991 when harvesting was regulated in the 1970s–1980s. Our result implies that the fishermen of Akita Prefecture might have avoided the 3-year fishing closure, which is much stricter than the 20%–30% reduction in the exploitation rate, if this reduction in exploitation had been conducted in a timely manner in the 1980s.

Since 1995, the NSJ fishermen of Akita Prefecture have implemented a total allowable catch (TAC) system, which is calculated by a constant exploitation rate of 0.5 for BNSJ aggregating off Akita Prefecture (i.e., not the entire BNSJ) (Sugiyama 1998). Other NSJ fishermen, i.e., those belonging to the offshore fisheries, did not participate in the TAC system. A TAC system requires consideration of both environmental conditions and all of the NSJ offshore fisheries, which caused the overfishing in the 1980s. On the other hand, all of the NSJ offshore fisheries set a lower limit to body length at first capture. This regulation could complement the TAC system, which is vulnerable to uncertainty about stock assessments (e.g., Walters and Parma 1996).

Our study investigated the mechanisms underlying NSJ dynamics and the impacts of environmental conditions and overfishing on NSJ, although the period studied is relatively short. Our results suggest that simultaneous dynamics of NSJ and WSJ have resulted from similarities in variations in winter temperatures for each stock, and that the difference in dynamics resulted from NSJ depletion caused by overfishing. Appropriate management strategies to prevent this depletion should allow improved biomass recovery while taking advantage of favorable environmental conditions, and should avoid overexploitation when stocks are already depleted by harvesting and unfavorable environmental conditions. In future, concrete management strategies must be developed under management objectives focused on coping with uncertainties, risk assessment, and the economic circumstances of NSJ fisheries (Butterworth and Punt 1999).

Our results should be of great value in determining the future direction of management strategies to prevent NSJ depletion and to rebuild NSJ.

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Does selective fishing conserve community biodiversity? Predictions from a length-based multispecies model

Marie-Joëlle Rochet, Jeremy S. Collie, Simon Jennings, and Stephen J. Hall

Abstract: This study challenges the widely held view that improved fisheries selectivity would always help to maintain marine biodiversity. Using a length-based multi-species model, we investigate the effects of selective versus nonselective fishing on fish communities. Both size and species selectivity are examined, and fishing effects on biodiversity are measured with three indices: (*i*) evenness, (*ii*) the number of collapsed species, and (*iii*) an index of size diversity. The model is parameterized for the Georges Bank and North Sea fish communities. The results suggest that there is no "optimal" size selectivity to maintain biodiversity: the effects of each exploitation pattern depend on the selectivity of the gear (i.e., the shape of the selection curve) relative to the available sizes. Catching a narrow range of species almost always reduced evenness and species richness more than taking the same catch from a broader range of species. In summary, neither selective nor nonselective fishing can be said to be generally preferable for conserving biodiversity; the outcome depends on the particular species composition and size structure of the community. Advice intended to inform management will need to be based on clear definitions of biodiversity, and unambiguous management objectives for biodiversity and the fishery.

Résumé : Cette étude remet en cause l'idée répandue qu'une amélioration de la sélectivité des pêches aiderait à protéger la biodiversité marine. Un modèle multi-spécifique en longueur est utilisé pour examiner les effets de pêches sélectives ou non sur des communautés de poissons. La sélectivité peut concerner soit la taille soit les espèces, et les effets de la pêche sont mesurés par trois indices : l'équitabilité, le nombre d'espèces surexploitées, et un indice de diversité des tailles. Le modèle est paramétré pour les communautés du Banc George et de la mer du Nord. Il n'y a pas de sélectivité par taille qui conserve mieux la biodiversité dans tous les cas : le meilleur patron d'exploitation dépend de la sélectivité de l'engin (c'est-à-dire, la forme de la courbe de sélection) par rapport aux tailles disponibles. Pour ce qui concerne la sélectivité par espèce, la sélection d'un petit nombre d'espèces réduit presque toujours davantage l'équitabilité et la richesse spécifique que si la même biomasse est prise en capturant toutes les espèces. En résumé, pêche sélective ou équitable ne peuvent pas être généralement considérées comme mieux à même de préserver la biodiversité : le résultat dépend de la composition spécifique et de la structure en taille de la communauté. Tout avis pour la gestion devra reposer sur des définitions claires de la biodiversité et des objectifs de gestion pour cette dernière et pour les pêcheries.

Introduction

Fishing gears are not perfectly selective; they generally catch a wider range of species and sizes of animals than intended. Part of the resulting by-catch can be landed and marketed, but there are two broad categories of unwanted by-catch that are usually discarded dead or dying: large-sized vertebrates such as turtles, dolphins, or sharks, which may be "charismatic", or threatened, or both; and, low-valued or prohibited size-ranges and species of fish. Both categories of by-catch are the subject of increasing concern, in both the public and the scientific community (Hall 1996; Lewison et al. 2004).

Avoiding by-catch requires more selective fishing, and improving selectivity is seen as an important tool to protect nontarget and vulnerable species (Pikitch et al. 2004), and to rebuild marine ecosystems (Worm et al. 2009). Gear technologists generally see their goal as "perfect gear selectivity" (Broadhurst 2008). "Improving selectivity" is generally understood as both achieving a "cleaner" catch of the target species or size, and targeting larger sizes or species with a higher commercial value. Two types of modifications are used to change fishing selectivity: those that exploit differences in behavior among species, thus improving species-selectivity; and those that mechanically sieve organisms

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according to their size and change size-selectivity (Broadhurst 2000).

While improved selectivity can help to balance exploitation rates with the productivity and abundance of component populations in mixed fisheries, improved selectivity can also lead to greater contrasts in production or biomass among components of the food web. These changes will modify food-web interactions, so it is necessary to consider whether the modified interactions would support or compromise intended management objectives. There is growing evidence that selective exploitation of species in food webs has led to changes in prey, predator, or competitor species. For example, changes in food webs have followed the depletion of apex predators (Polovina et al. 2009), intermediate consumers (Bundy et al. 2009), whales (Springer et al. 2003), and forage fish (Hjermann et al. 2004). Thus, if an objective of management is to maintain the structure and function of ecosystems, then more selective fishing may not support this objective (Hall 1996; Zhou 2008).

With the widespread adoption of an Ecosystem Approach to Fisheries, management authorities are starting to define objectives for biodiversity. Biodiversity, in the broadest sense, is the variety, quantity, and distribution of life, but relatively few aspects of biodiversity have been used as management objectives (Greenstreet 2008), with the main focus on the population status of vulnerable species that are impacted by fisheries (Lewison et al. 2004). Gear technology (Jennings and Revill 2007), combinations of gears with different selectivities (Hinke et al. 2004), or spatial management approaches (Branch and Hilborn 2008; Pikitch et al. 2004) have been proposed to reduce mortality rates on vulnerable species. However, little has been done to consider options for more effective management of other aspects of biodiversity that might be considered as management targets. These targets include various aspects of species diversity within communities, such as evenness and total species numbers, all of which are closely related to ecosystem functioning (Purvis and Hector 2000).

So how selectively should we harvest our oceans, if we are to conserve these aspects of biodiversity? The answer to this question requires, among other things, an assessment of the effect of selective fishing on marine community biodiversity. Here, we aim to develop a general, model-based comparison of the effects of changing the selectivity and rates of fishing on biodiversity. Both the choice of target and the degree of selectivity interact to determine the effect. In simulations with a size-based model, it has been predicted that selectively fishing a narrow size-range creates instability in the biomass spectrum and decreases size-diversity, while unselective fishing does not (Rochet et al. 2009). This effect is more pronounced when larger rather than smaller sizes are selectively fished. However, this size-based approach ignored that species life histories may make a difference in population and food web impacts (Schindler et al. 2002). Moreover, it does not consider the consequences of fishing selectivity on stock abundances, nor on other facets of species diversity. To predict the effects of size- or species-selectivity on community biodiversity, a model incorporating both size and species identity is required.

To mimic the community responses to fishing, we parameterize an existing multi-species length-based model (Hall et al. 2006) with the species life histories and diet matrices for (*i*) Georges Bank, in the northwest Atlantic, and (*ii*) the North Sea. Fishing effects on species diversity are measured by indices of richness and evenness, and one that describes size diversity. We use size diversity because body size is closely related to many ecological functions (Woodward et al. 2005), and the diversity in size structure may provide one proxy for functional diversity. To describe the more social and economic consequences for fisheries, we also report the predicted effects of fishing on the catch weight (mass) and value.

When comparing selectivity patterns, one challenge is to decide which fishing pressures are comparable. Thus, in addition to comparing fishing effects at various mortality rates, we also compare them for a given catch level, based on mass or value. Here, we first describe the model, parameterization, and validation criteria. Second, we present fishing scenarios based on size or species selectivity. Third, we define the community metrics used to gauge fishing effects on biodiversity and catch. Fourth, we present simulation results, and examine whether they are similar across the two communities. Finally, we discuss how these results might influence advice on developing exploitation strategies to meet specified management objectives for biodiversity.

Materials and methods

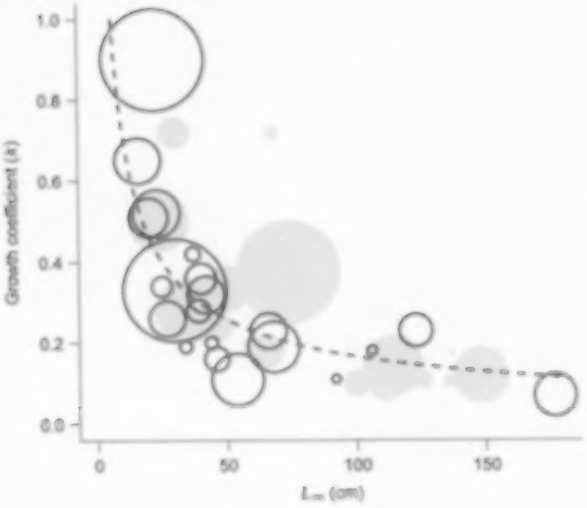
Community model

A length-based multispecies model (LeMANS) (Hall et al. 2006) was used to describe the population dynamics of 21 species with defined life-histories, structured in fifteen 10-cm length classes. In this model, animals grow towards an asymptotic size following the von Bertalanffy growth model, and reproduce according to a Ricker stock–recruit relationship. Mortality includes three components: (1) nonpredation mortality ($M1$) is a U-shaped function of length; (2) predation mortality ($M2$) depends on the predator–prey size ratio, predator abundance (with a Holling type-II functional response), and a diet matrix that describes who eats whom; (3) fishing mortality (F) depends both on species (some species are fished and others are not) and size, based on a logistic selection curve. In this application of the model we also used a normal selection curve (see below).

To reduce predation mortality on the smallest size class, two refinements were made to the predation component of the length-based model in this study. The parameters of the predator size-preference function were changed from $\mu = -3.5$, $\sigma = 1$ (Hall et al. 2006, Fig. 1*b*) to $\mu = 0.5$, $\sigma = 2$. The result is a broader curve with preference for slightly larger sizes. These parameters give a preferred prey:predator mass ratio of 1:33, which is comparable with that measured in empirical feeding studies (Floeter and Temming 2005).

The equation for predation mortality contained a term "other food" to account for the nonmodeled prey species in the fish diets (Hall et al. 2006, eq. 8). The model dynamics were found to be very sensitive to the amount of "other food": too little, and some prey species would go extinct; too much, and predation mortality on the modeled prey species was negligible. To remove this sensitivity to other food, we introduced a size-structured "forage species" to represent small fish and invertebrates in the smallest size classes,

Fig. 1. Relationship between the von Bertalanffy growth coefficient (k) and asymptotic length (L_∞) among fish species on George Bank (filled circles) and in the North Sea (open circles). Circle area is proportional to the maximum biomass of each species (S_{max}). The broken line is the fitted relationship between k and L_∞ from Gislason et al. (2010).



in which predation mortality is the highest. The generic life-history parameters of the forage species were patterned after the smallest fish species in the community (Table 1). The Ricker productivity parameter (α) was set at 400, a high value that ensured a high biomass of forage species that would not be depleted by predation. All predator species in the model were also assumed to eat the forage species, which were not fished.

Model parameterization and validation

Georges Bank

The parameterization used in Hall et al. (2006) was unchanged, except for the parameters of the stock–recruit relationship, which were recalculated from updated abundance data. Because stock–recruit relationships do not exist for most of the 21 species, we used a meta-analytic approach, whereby the density-dependent parameter of the stock–recruit relationship (β) was related to the maximum spawning stock biomass of each species (Hall et al. 2006, Fig. 1*b*). In this parameterization we calculated the maximum biomass values from the Georges Bank trawl-survey data that were analyzed by Steele et al. (2007). We selected the decade from 1963–1972 as representing lower fishing mortality rates than the later period of heavy exploitation. To guard against extreme values, we chose the 90% percentile, which means that we selected the second highest biomass value for each species between 1963–1972. Updated maximum spawning biomass (S_{max}) ranged from 0.4–250 kilotonnes instead of 10–465 kilotonnes; S_{max} of the forage species was set at 5 megatonnes (Mt), the smallest value that prevents prey species from collapsing with no fishing.

North Sea

Life-history parameters (Table 1) of 21 fish species in the North Sea and their corresponding diet matrix (Table 2) were assembled from published sources. The model comprised eighteen 10-cm length classes to accommodate the asymptotic length of pollock *Pollachius virens* (Table 1, North American common names are used for consistency with the Georges Bank fish community). Estimates of β, the density-dependent stock recruitment parameter, were derived with the meta-analytical approach described above (Hall et al. 2006). The maximum spawning-stock biomass from 1980–2004 was derived from a combination of stock-assessments and trawl-survey data for non-assessed species. Stock assessments were available for 9 of the 21 species. For the remaining species, biomass estimates were taken from the International Bottom Trawl Survey (Quarter 1) and adjusted for species-specific catchability (Table 1). For the North Sea, L_{mat} is the length of full maturity, not 50% maturity. Lacking a maturity ogive for the North Sea fishes, we set the slope of the maturity ogive to a high value (α = 10) for all species to create "knife edge" maturity. Maximum spawning biomass (S_{max}) of the forage species was set at 50 Mt, reflecting the larger area of the North Sea and greater fish biomass compared with Georges Bank.

The distribution of asymptotic length (L_∞) and growth coefficients (k) across species corresponds with the relationship expected from life-history theory (Fig. 1) (Gislason et al. 2010). In the North Sea the community biomass is concentrated in small- and intermediate-sized species (<70 cm), while Georges Bank biomass is dominated by intermediate- and larger-sized species. The 21 species included in LeMANS dominate biomass in the whole communities. The difference in size distributions is also a characteristic of the full Georges Bank and North Sea fish communities (Collie and Rochet 2010).

Key-run specification

Key-runs were created with six rates of fishing mortality, F_{full}, on all fished species from 0 to 1. The parameterization that best mimicked the effects of fishing at the community level was selected based on four criteria: (*i*) comparing the total biomass of the fish community over a range of fishing mortality with survey-based biomass estimates; (*ii*) comparing biomass ranked by species (which is related to evenness), estimated with LeMANS with F_{full} = 0.2, with ranked biomass from the survey. This is an internal test of consistency because the survey biomass estimates were used to derive the stock-recruit β parameter; (*iii*) comparing the slopes of size spectra estimated with the model with the slopes of survey-derived size spectra; (*iv*) Comparing estimates of predation mortality ($M2$) from LeMANS with the $M2$ estimates of selected prey species from Multispecies Virtual Population Analysis (MSVPA). We compared the average $M2$ for ages 0–1 from MSVPA to the annual $M2$ averaged over the corresponding length range in LeMANS, as calculated from the von Bertalanffy growth parameters.

Fishing selectivity

The effects of size and species selectivity were investigated separately. Fishing mortality in the model depends on

Table 1. Species-specific parameters used for North-Sea community.

Scientific name	Common name	k (year^{-1})	L_∞ (cm)	L_{mat} (cm)	a	b	S_{max} (tonnes)	ϕ_i
—	Forage species	0.10	20	13	0.005	3.0	50×10^6	0
Sprattus sprattus	Sprat	0.65	16	12	0.002112	3.4746	348 307	1
Trisopterus minutus	Norway pout	0.51	20	15	0.009200	3.0265	247 644	0
Ammodytes spp	Sandeel	0.90	22	11	0.001243	3.3200	1 735 847	1
Trisopterus esmarkii	Poor cod	0.52	23	15	0.005180	3.1170	371 336	1
Hippoglossoides platessoides	Long rough dab	0.34	25	15	0.004400	3.2309	69 720	0
Limanda limanda	Dab	0.26	27	13	0.007400	3.1128	214 644	0
Clupea harengus	Atlantic herring	0.33	30	25	0.007420	3.0256	1 759 000	1
Trachurus trachurus	Horse mackerel	0.19	34	19	0.003400	3.2943	25 600	1
Microstomus kitt	Lemon sole	0.42	37	27	0.025500	2.7643	35 340	1
Solea vulgaris	Sole	0.28	39	25	0.003600	3.3133	89 700	1
Scomber scombrus	Mackerel	0.36	40	26	0.003001	3.2900	155 038	1
Merlangius merlangus	Whiting	0.32	42	20	0.005180	3.1170	231 716	1
Glyptocephalus cynoglossus	Witch flounder*	0.20	44	29	0.001050	3.4950	26 793	1
Eutrigla gurnardus	Gurnard	0.16	46	23	0.006200	3.1003	97 068	0
Pleuronectes platessa	Plaice	0.11	54	27	0.021500	2.7901	441 924	1
Amblyraja radiata	Starry ray	0.23	66	46	0.040900	2.8965	215 644	0
Melanogrammus aeglefinus	Haddock	0.19	68	34	0.005580	3.1330	431 386	1
Leucoraja naevus	Cuckoo ray	0.11	92	59	0.038700	2.9591	12 522	0
Lophius piscatorius	Monkfish	0.18	106	61	0.015300	2.9979	15 045	1
Gadus morhua	Atlantic cod	0.23	123	70	0.006530	3.0970	181 697	1
Pollachius virens	Pollock*	0.07	177	55	0.010000	2.9620	291 000	1

Note: Parameter definitions are as follows: k and L_∞ are parameters of the von Bertalanffy growth equation; L_{mat} is length at maturity; a and b are coefficients of the mass (g) – length (cm) relationship; S_{max} is the maximum spawning stock biomass; ϕ_i indicates fished (1) and unfished (0) species. Sources: Coull et al. 1989; ICES 2005*b*; Jennings et al. 1998, 1999.

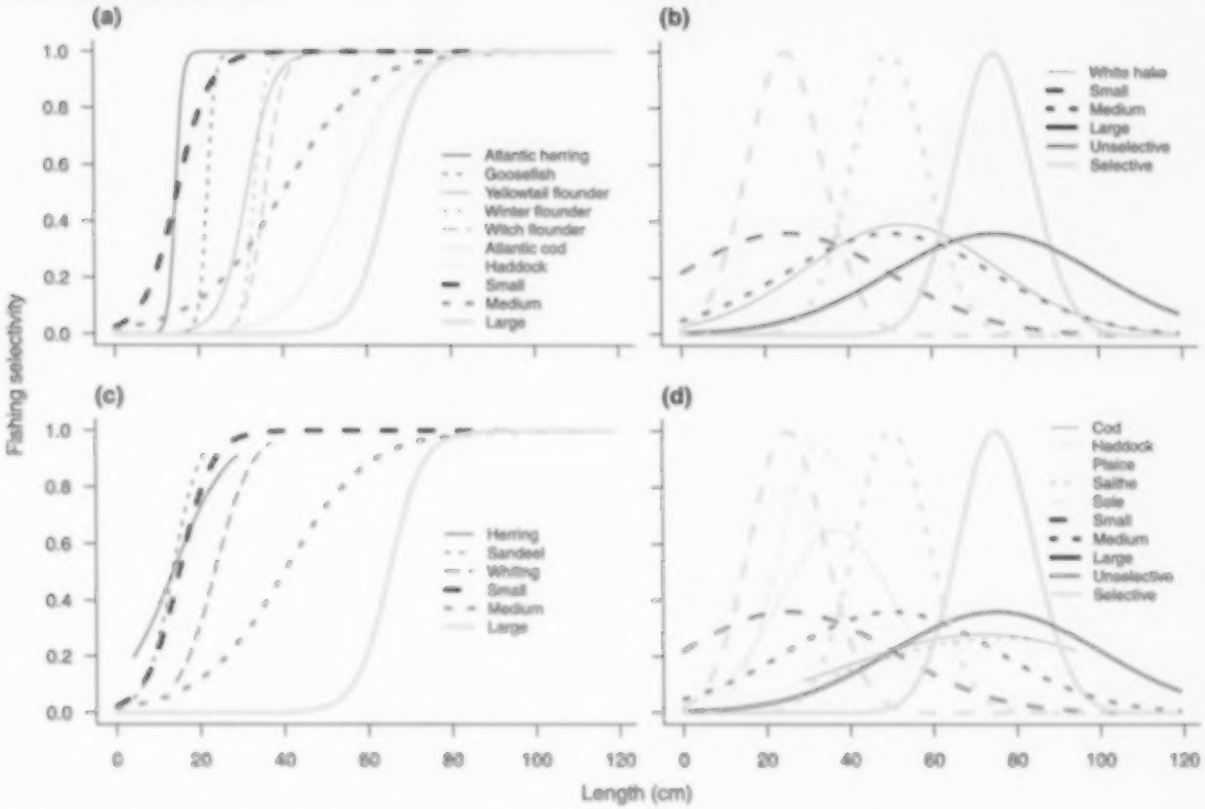
*The North American common names are used for consistency with the Georges Bank fish community.

Table 2. The food-web matrix for the 21 North-Sea species.

	Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
	Prey species																					
0	Forage species	0	0	0	0	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1
1	*Sprattus sprattus*	0	0	0	0	0	0	1	1	0	0	1	1	0	1	0	0	1	0	0	1	1
2	*Trisopterus esmarkii*	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	1	1	1	1	1	1
3	*Ammodytes* spp	0	0	0	0	0	1	1	1	0	0	1	1	0	1	1	1	1	1	0	1	1
4	*Trisopterus minutus*	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0
5	*Hippoglossoides platessoides*	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
6	*Limanda limanda*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0
7	*Clupea harengus*	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1	0	1	0	1	1
8	*Trachurus trachurus*	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	1	1
9	*Microstomus kitt*	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
10	*Solea vulgaris*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
11	*Scomber scombrus*	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1
12	*Merlangius merlangus*	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	1	1	1
13	*Glyptocephalus cynoglossus*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
14	*Eutrigla gurnardus*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
15	*Pleuronectes platessa*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
16	*Amblyraja radiata*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17	*Melanogrammus aeglefinus*	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	1	0	1	1	1
18	*Leucoraja naevus*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19	*Lophius piscatorius*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	*Gadus morhua*	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	1	1	1	1
21	*Pollachius virens*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0

Note: Diet of monkfish and sole unavailable for North Sea, borrowed from Celtic Sea. Diet of cuckoo ray incomplete, borrowed from starry ray for items not available. Sources: Daan et al. 1993; ICES 2005*a*; Pinnegar and Stafford 2007; Segers et al. 2007.

Fig. 2. Size-selection curves simulated in the model (bold lines, see parameters in Table 3) compared with curves estimated empirically (thin lines) for Georges Bank (top) and North Sea (bottom) species. (*a*,*c*) S-shaped small, black; S-shaped medium, dark gray; S-shaped large, light gray. (*b*,*d*) Bell-shaped targeting small fish, dashed lines; medium fish, dotted lines; large fish, unbroken lines; selectively, light grey; or unselectively, dark grey.



both size and species independently: $F_{l,i} = F_{\text{full}}\,\phi_i\,S(l)$, where $F_{l,i}$ is the fishing mortality of length class l, species i; F_{full} is the annual fishing mortality rate for a fully recruited fish; ϕ_i is a binary variable indicating whether species i is fished, and $S(l)$ is a selection curve as a function of length. In the original model, size-selection was a logistic function:

$$S(l) = \frac{1}{1 + \exp[-\eta(l - L_{F50})]}$$

with η a slope parameter and L_{F50} the size at 50% selection by the fishery. This selection model defines a lower bound: the larger the size at 50% selection, the larger the bound and the more selective the fishery (Fig. 2*a*). We modeled a less selective fishery, partly avoiding intermediate sizes with a "medium" selection curve having a low slope. However, at the community level, an S-shaped function might not be realistic, and a bell-shaped selection curve might be more representative of the multispecies catches relative to video estimates of total abundance (Wells et al. 2008). In addition, single-species logistic selection curves are often used for trawls, while bell-shaped selection curves might be more relevant for gill-nets or hooks (Millar and Fryer 1999). Thus, besides the logistic selection curve, a bell-shaped, normal selection curve was used:

$$S(l) = \frac{1}{\sigma_F\sqrt{2\pi}}\exp\left[-\frac{1}{2}\left(\frac{l - \mu_F}{\sigma_F}\right)^2\right]$$

where μ_F is the target length, and σ_F the width of fishing mortality at size, or inverse precision of the target. In this application, fishing intensity was divided by the maximum density for the most selective selection curve (0.0443) so that for selective fishing, fishing mortality at the target size is F_{full}. Less selective fishing implied a lower peak mortality (Fig. 2*b*) with the same cumulated F over all length classes fished. Below, we use the terms "S shaped" to refer to the logistic curve and "bell shaped" to refer to the normal selection curve.

The size-selection curves used in the model simulations were parameterized to be comparable with selection curves derived from stock assessments for a subset of the species (Fig. 2). Relative fishing mortality at age was extracted for the most recent decade and converted, with the corresponding von Bertalanffy growth parameters, to relative fishing mortality at length. For each species, either a logistic or normal curve was selected based on the best goodness-of-fit to the relative fishing mortality rates. Seven of the Georges Bank species had logistic size-selection curves (Fig. 2*a*). Most had relatively high slope parameters, except cod,

Table 3. Parameters of the size-selection curves for the nine fishing scenarios simulated in the model.

	Bell-shaped, selective		Bell-shaped, nonselective		S-shaped	
Target / bound	σ_s	μ_s (cm)	σ_s	μ_s (cm)	η	L_{s50}(cm)
Small	9	25	25	25	0.25	15
Medium	9	50	25	50	0.1	40
Large	9	75	25	75	0.25	65

which was more similar to a "medium" curve. The length at 50% selection ranged from 15 cm for herring to 55 cm for cod and haddock. Spiny dogfish (not plotted) had knife-edge selection at 75 cm. One species, white hake, had a bell-shaped selection curve that was very similar to a medium unselective curve (Fig. 2*b*). In the North Sea three species had S-shaped selection curves with high slope and small length at 50% selection (Fig. 2*c*). Five species had a bell-shaped selection curve, in which width was correlated with mode: larger species seemed to be exploited less selectively (Fig. 2*d*). Overall, the set of size-selection curves used in the simulations covers the range of observed selection curves.

For both logistic and normal size selection, nine contrasting scenarios of selective/nonselective fishing were simulated (Table 3) along with a series of increasing rates of fully recruited fishing mortality. Because the selectivity curves have various shapes, however, combinations with fishing mortality will exert pressures on the community that are not directly comparable. Therefore, community metrics were examined as a function of either F_{full} or total catch, taken as a measure of fishing pressure at the community level. Total catch was measured either as mass or in value (estimated as mass multiplied by average price per pound or kilogram). Price data were obtained for Georges Bank from Eric Thunberg (Northeast Fisheries Science Center, NOAA-NMFS, Woods Hole, Massachusetts, personal communication 2009) and for the North Sea from Fabienne Daurès (IFREMER, Brest, France, personal communication 2009) for sandeel and sprat, and FranceAgriMer (2010) for the other species. In this analysis, species selectivity was set as in the key-runs: there were four unfished species on Georges Bank and seven in the North Sea, including the forage species.

Species selectivity was analyzed by varying the number of species fished, that is, by manipulating the ϕ_i parameters: the target set is the set of species with $\phi_i = 1$. For these species-selection trials, the maximum fishing mortality was set at 0.4. Target sets of increasing number were created randomly; each number was repeated at least 21 times with different random sets, and the resulting distributions of community metrics were compared. The number of samples was increased until the patterns stabilized, that is, up to 250 for intermediate numbers of species (8–13); in these cases the number of possible sets increases exponentially (up to 350 000 for 10 and 11 species). Reference levels for community metrics in unselectively fished communities were calculated as follows: for each target number, we calculated median total catch, and identified the fishing mortality rate (F^*_{full}) that would yield at least that total catch, if all species were fished. The value of each community index with all species fished at F^*_{full} was then used as a reference value. In this analysis size selectivity was set as in Hall et al. (2006), so that most sizes were targeted (logistic selection curve with $L_{s50} = 25$ cm and $\eta = 0.25$).

Measuring fishing effects

Fishing effects at the community level were measured with three diversity measures, two for species diversity and one for size diversity. For measuring species diversity in simulated communities with fixed numbers of species (N), richness has little meaning, but a strong reduction in population size of a given species may amount to a functional loss of that species. The change in richness was therefore described by the number of species collapsed, where "collapsed" is defined as a reduction in biomass of 90% or more from the unfished level (e.g., according to the International Union for the Conservation of Nature (IUCN) criterion: species are listed as critically endangered if their population numbers were reduced by 90% or more over a specified time-period). In addition, a metric of the evenness of the distribution of individuals among species is needed. Simpson's reciprocal evenness index $E_{1/D} = 1/(DN)$ was used, where Simpson's D measures the probability that two random individuals belong to different species (Smith and Wilson 1996). For measuring size diversity, a similar index with size classes instead of species is inappropriate, because it does not account for size classes being ordered; so a metric including some measure of distance, like the taxonomic diversity metrics of Clarke and Warwick (1998), is required. We used average size-distance between two random individuals, giving size diversity as

$$\Sigma = \frac{\int_{x_{min}}^{x_{max}} \int_{y_{min}}^{y_{max}} d(x,y)u(x)\exp(x)u(y)\exp(y)dxdy}{\int_{x_{min}}^{x_{max}} \int_{y_{min}}^{y_{max}} u(x)\exp(x)u(y)\exp(y)dxdy}$$

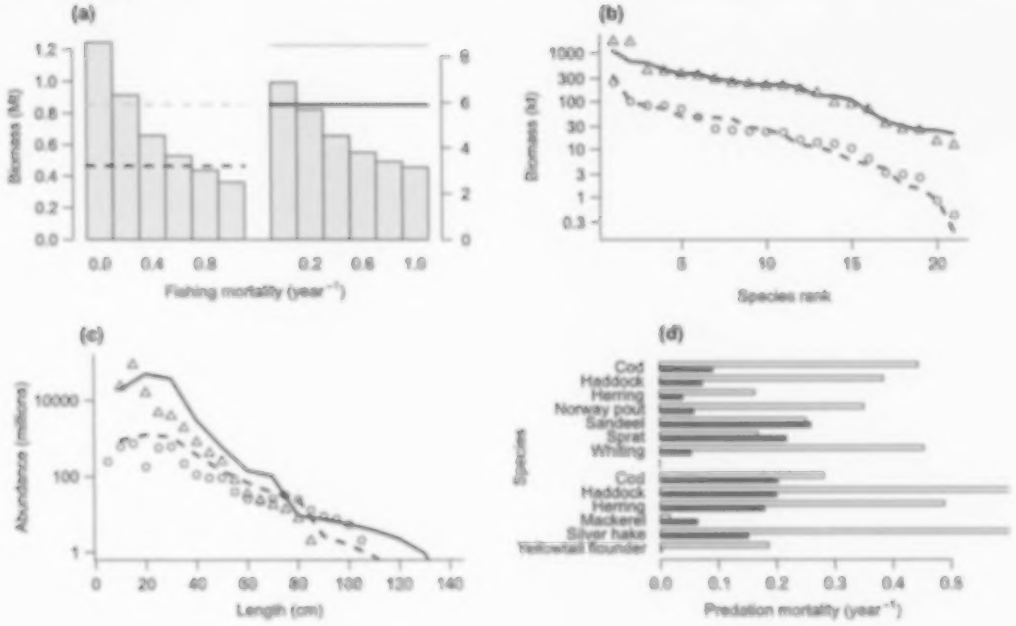
where $u(x)$ is the number of individuals with size x; $d(x, y) = 1 - \exp(-\delta|x - y|)$ measures the distance between two sizes x and y, and δ is a shape parameter determining the rate at which the distance will reach 1 (Rochet et al. 2009). The size diversity of a linear size spectrum decreases as its slope decreases (as size spectra have negative slopes, this means that steeper spectra are less diverse); bumpy size spectra have lower size diversity than regular ones.

Results

Model key runs

Both key-runs had acceptable levels of agreement with empirical measures of community structure (Fig. 3). The model estimates of Georges Bank biomass over a range of fishing mortality from 0.2 to 0.7 spanned the range of survey biomass, calculated either over the entire time series or for the decade 1963–1972, when fish biomass was lower (Fig. 3*a*). For the North Sea, total biomass of the fish community estimated with LeMANS was generally lower than the biomass of 11 commercial fish species estimated from stock assessments for the years 1983–1985 (Sparholt 1990).

Fig. 3. Key-run diagnostics for Georges Bank (dashed lines, open circles) and the North Sea (unbroken lines, open triangles). (*a*) Total biomass of the fish community at six levels of fishing mortality (F_{full}, bars) compared with survey-derived biomass estimates (lines) for Georges Bank (left): averaged over 1963–2002 (grey) and 1963–1972 (black) and the North Sea (right): quarters 1 (black) and 3 (grey). (*b*) Ranked biomass of each species estimated by LeMANS with F_{full} = 0.2 (lines) compared with the biomass estimates that were used to estimate the β stock–recruit parameter (points). (*c*) Size spectra estimated by LeMANS with F_{full} = 0.2 (lines) compared with average survey-derived size-spectra (points). (*d*) Average predation mortality for ages 0–1 estimated by LeMANS (black bars) and by MSVPA (grey bars) for (top) seven of the 21 North Sea species (ICES 2005a) and (bottom) six of the 21 Georges Bank species (Tsou and Collie 2001); haddock M_2 = 0.65, silver hake M_2 = 1.44.



The estimates are in better agreement for quarter 1 than quarter 3, but only for modeled fishing mortality less than 0.2 (Fig. 3*a*). Biomass ranked by species, estimated with LeMANS with F_{full} = 0.2, agreed well with the survey ranked biomass (Fig. 3*b*). This criterion ensured that the evenness in the modeled community is similar to that in the real fish community. In the North Sea exceptions occurred for the two most abundant (herring and sandeel) and two least abundant (cuckoo ray and monkfish) species, with LeMANS predicting a more even distribution of biomass (Fig. 3*b*). The estimated size spectra matched the survey size spectra quite well, although in the North Sea, LeMANS slightly overestimated abundances for lengths > 25 cm (Fig. 3*c*). The estimates of predation mortality (*M*2) from LeMANS are the same order of magnitude as the *M*2 estimates of six prey species from an MSVPA of the Georges Bank fish community (Tsou and Collie 2001), but they differ for particular species (Fig. 3*d*). For example, the *M*2 estimates are in good agreement for Atlantic cod, but the MSVPA estimates are considerably higher for yellowtail flounder, haddock, silver hake, and Atlantic herring. In LeMANS, the selectivity for prey species depends only on their size, whereas MSVPA includes a species-preference parameter. Therefore in LeMANS it is difficult to fine-tune the *M*2 values for particular prey species. For the North Sea, LeMANS *M*2 values are in good agreement for the smaller prey species (sandeel and sprat), but are lower for larger species (cod, haddock, and whiting). In any case, predation mortality cannot be directly observed, and these are all model estimates. In summary, the diagnostic criteria were met for both the Georges Bank and North Sea fish communities apart from minor differences in total biomass. Both key-runs were accepted as the bases for subsequent selectivity simulations.

Size selectivity

The effects of mortality depend on the shape of the selectivity function (Fig. 4; Table 4). On Georges Bank with a logistic selection curve, the highest catch could be obtained by the "medium" selection ogive and F_{full} = 1, while catch peaked for F_{full} = 0.4 when small fish were fished. With a bell-shaped selection curve, high catches were obtained regardless of selectivity when large or medium-sized fish were targeted; when the target was small, less than half the maximum catch could be obtained, and still less when fishing selectively (Fig. 4*g*). Evenness was little affected by targeting large fish, and decreased when fishing mortality increased if medium or small fish were targeted (Figs. 4*a* and 4*e*). The number of collapsed species increased when fishing mortality increased, more when small sizes were targeted, irrespective of selectivity (Figs. 4*d* and 4*h*). More species were collapsed with the logistic selection curve, illustrating the higher fishing pressure on the community

Fig. 4. Effects of increasing fishing mortality on community metrics for Georges Bank when size-selectivity is (*a–d*) S-shaped (small, black lines; medium, dark gray lines; large, light gray lines) or (*e–h*) bell-shaped (targeting small fish, dashed lines; medium fish, dotted lines; or large fish, unbroken lines; selectively, light grey; or unselectively, dark grey). F_{full} is fully recruited fishing mortality. (*a,e*) Evenness, (*b,f*) size diversity, (*c,g*) total catch in hundred kilotonnes, (*d,h*) number of species collapsed.

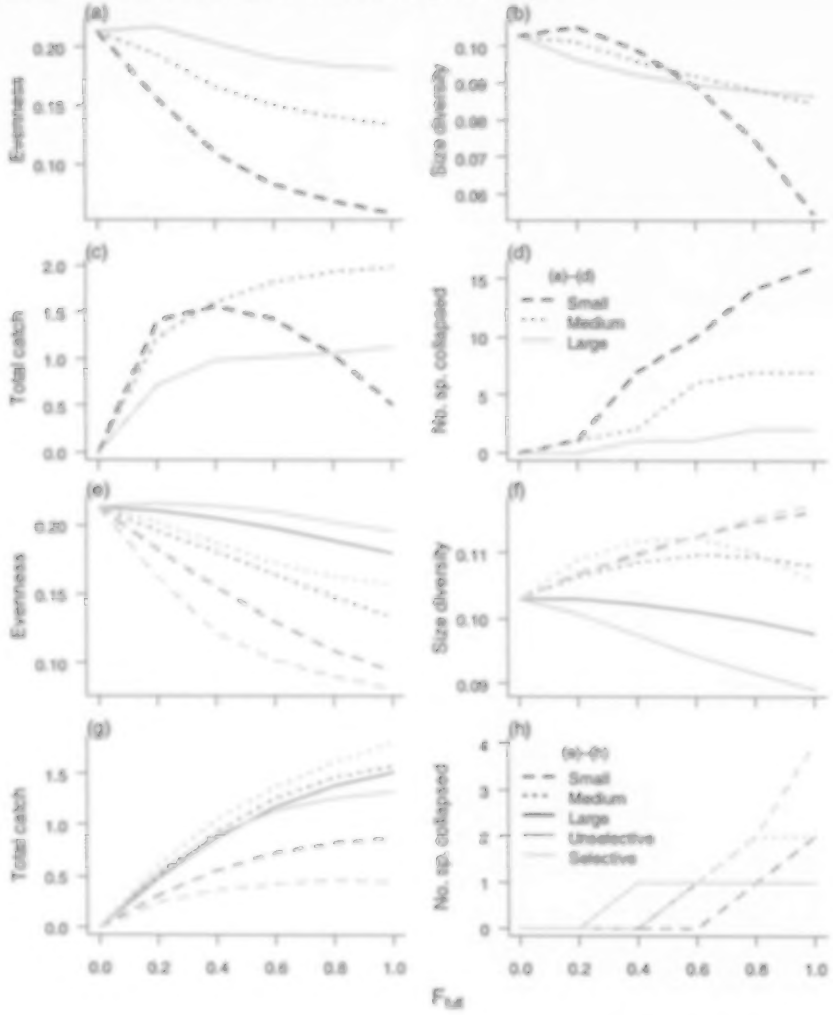
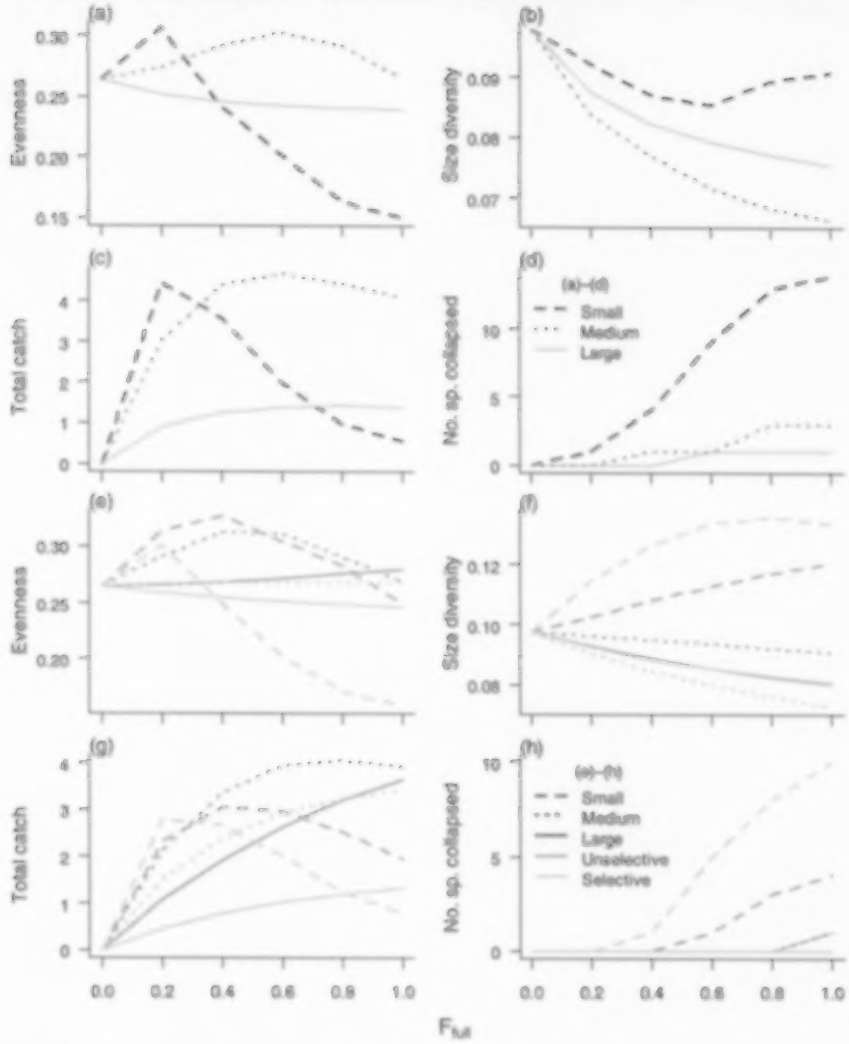


Table 4. Summary of size-selectivity simulation results.

Metric	NS, bell-shaped selectivity			NS, S-shaped selectivity			GB, bell-shaped selectivity			GB, S-shaped selectivity		
	S	M	L	S	M	L	S	M	L	S	M	L
Evenness	$\cap^{S}$	$\cap^{S}$	—^{U}	$\cap$	$\cap^{*}$	—	$\searrow^{U}$	$\searrow^{S}$	$\searrow^{S}$	$\searrow$	$\searrow$	$\searrow^{*}$
Size diversity	$\nearrow^{S}$	$\searrow^{U}$	$\searrow^{S(U)}$	$\cup^{*}$	$\searrow$	$\searrow$	$\nearrow^{S(U)}$	$\cap$	$\searrow^{U}$	$\searrow$	$\searrow^{*}$	$\searrow^{*}$
Total catch	$\cap^{U}$	$\nearrow^{U}$	$\nearrow^{U}$	$\cap$	$\cap^{*}$	$\nearrow$	$\nearrow^{U}$	$\nearrow^{S}$	$\nearrow^{U}$	$\cap^{*}$	$\nearrow^{*}$	$\nearrow$
No species collapsed	$\nearrow^{U}$	$\nearrow^{S(U)}$	—^{S}	$\nearrow^{*}$	$\nearrow$	—	$\nearrow^{U}$	$\nearrow^{S(U)}$	$\nearrow^{S}$	$\nearrow^{*}$	$\nearrow$	$\nearrow$

Note: Predicted trends in community metrics in the North Sea (NS) and Georges Bank(GB) with increasing fishing mortality, under various fishing regimes (S, small; M, medium; L, large). Northeast pointing arrow ($\nearrow$), increase; southeast pointing arrow ($\searrow$), decrease; —, unchanged; $\cap$, dome-shaped; $\cup$, U-shaped. For bell-shaped selectivity, each metric varied in the same direction under selective and unselective fishing, but with different slopes. Superscript indicates fishing selectivity that maximizes each metric under the fishing regimes (U, nonselective; S, selective for bell-shaped selectivity; asterisk (*), for S-shaped selectivity). For S-shaped selectivity, the outcome depends on fishing intensity: entries in the table are for high F_{full} (>0.7).

Fig. 5. Effects of increasing fishing mortality on community metrics for the North Sea when size-selectivity is (*a–d*) S-shaped (small, black lines; medium, dark gray lines; large, light gray lines) or (*e–h*) bell-shaped (targeting small fish, dashed lines; medium fish, dotted lines; or large fish, unbroken lines; selectively, light grey; or unselectively, dark grey). F_{full} is fully recruited fishing mortality. (*a,e*) evenness, (*b,f*) size diversity, (*c,g*) total catch in megatonnes, (*d,h*) number of species collapsed.

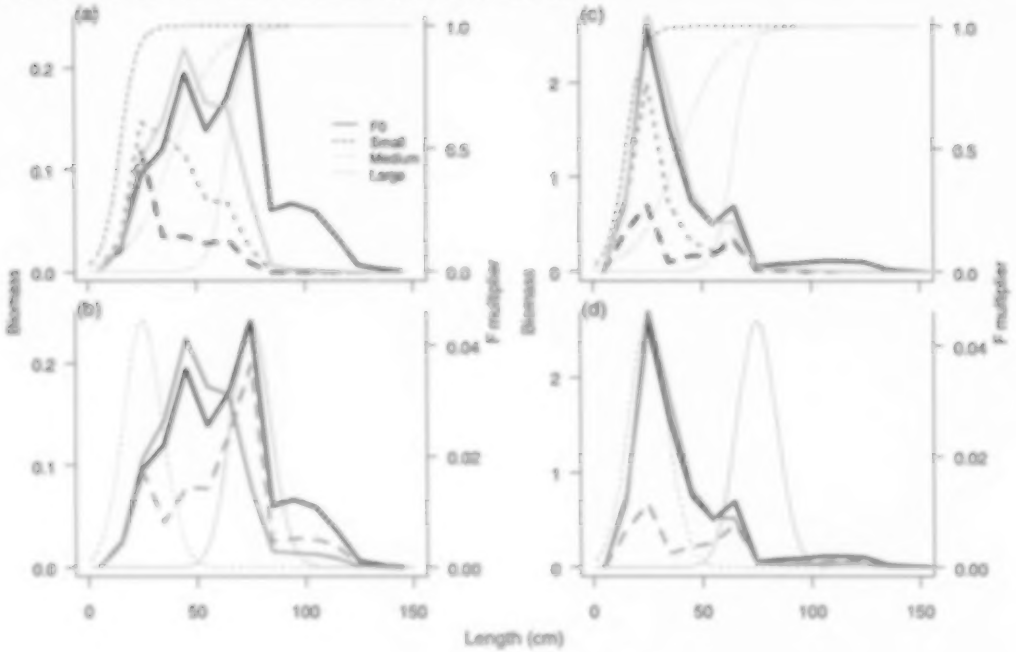


when this model is used. Size diversity decreased when fishing pressure increased with the logistic selection curve (Fig. 4*b*) or when large fish were targeted (Fig. 4*f*), but increased with the bell-shaped selection curve when small or medium fish were targeted (Fig. 4*f*).

By way of contrast, in the North Sea, with an S-shaped selection curve, high catches could be obtained either with a "small" or "medium" selection ogive, but when large fish were targeted, catches remained low, regardless of overall fishing pressure (Fig. 5*c*; Table 4). Also, when targeting large fish, total biomass and average mass (not shown) of fish in the community remained unchanged by fishing, as large sizes are mostly absent from the North Sea. Size diversity was highest when small fish were fished (Fig. 5*b*). With bell-shaped selectivity curves, maximum total catch was reached when targeting medium-sized fish unselectively; large catches could also be taken by targeting large-sized fish unselectively or medium-sized fish selectively (Fig. 5*g*). Size diversity increased with increasing fishing pressure when small sizes were targeted, while it slightly decreased when larger sizes were targeted (Fig. 5*f*). Noticeably, evenness was always higher when fishing unselectively than selectively, irrespective of the size targeted (Fig. 5*e*). Evenness was highest when small fish were exploited unselectively, and lowest when small fish were exploited selectively, because in this case some species, including sandeel, herring, horse mackerel, witch flounder, and plaice, were lost from the system (Fig. 5*h*).

These results reflect the shapes of the size spectra of the model-communities (Fig. 6): on Georges Bank there is little

Fig. 6. Biomass size-spectra of simulated communities in (*a*,*b*) Georges Bank or (*c*,*d*) North Sea with S-shaped (*a*,*c*) or bell-shaped (*b*,*d*) selectivity. Biomass in megatonnes. Bold lines show the biomass spectra in unexploited communities (black) or in communities fished with $F_{full} = 0.8$: selective fishing of small fish, dashed lines; selective fishing of large fish, unbroken lines; S-shaped small, black; medium, dark gray; large, light gray. Thin lines show the corresponding size selection curves.



biomass in the small size-classes, thus selectively targeting them cannot yield a high catch. Clearly the S-shaped selection curve with a small size at 50% selection amounts to catching almost everything in the community, and the resulting fishing pressure at the community level is high; it is the only selection pattern that potentially leads to community overfishing. Size diversity decreased with increasing fishing pressure with the logistic selection curve, owing to the loss of large fish (Fig. 6*a*), but increased with the bell-shaped selection curve (Fig. 6*b*); the exception being when large fish were targeted. In this case, the depletion in large fishes released small fishes from predation (Fig. 6*b*).

The unfished model community for the North Sea was dominated by small fishes (Figs. 6*c* and 6*d*). Size diversity increased at high fishing pressures, because the size spectrum was more regular, owing to the depletion of the small-size peak (Fig. 6*c*). Only small catches could be taken by targeting large fish selectively, owing to the small overlap between the size spectrum and the selection curve (Fig. 6*d*). Targeting small sizes resulted in decreased abundance at all sizes, and the spectrum became less bumpy, thus size diversity increased with increasing fishing pressure. When larger sizes were targeted, size diversity decreased because the spectrum was steeper (Fig. 6*d*).

When community metrics were plotted against total catch, patterns depended on the ecosystem and the shape of the selection curve (Fig. 7). On Georges Bank with an S-shaped selectivity, evenness and size diversity decreased as catch increased (except with "small size selection", where a loop is observed, owing to decreasing catch for high fishing mortality; Figs. 7*a* and 7*c*). With a bell-shaped selectivity, evenness decreased more steeply with catch when smaller fish were targeted; nonselective exploitation of small fish resulted in the steepest decline, while nonselective exploitation of large fish led to the least change. Targeting small fish maximized size-diversity and did not yield large catches, but nonselective exploitation of medium sizes led to high catches and high size diversity (Fig. 7*d*). The difference in patterns is explained by the overlap between the size spectrum and the selectivity curves (Fig. 6); small sizes have together the highest species richness and a relatively low biomass. When small sizes are targeted, most of biomass in the small size-range is removed and consequently the impact on the community is higher than for any other strategy. By contrast, in the North Sea, evenness and size diversity were maximized when lightly fishing small fish (S-shaped selection curve, Figs. 7*e* and 7*g*). With a bell-shaped selectivity curve evenness was highest with selective exploitation patterns (targeting small or intermediate sizes), but size diversity was maximized by targeting small fish (whether selectively or not, Figs. 7*f* and 7*h*). Using the value of total catch instead of mass as an index of fishing pressure yielded very similar figures (see supplementary data,[2] Fig. S1). In both communities a combination of high catches, high evenness and high size diversity was best obtained by fishing

[2] Supplementary data for this article are available on the journal Web site (http://cjfas.nrc.ca).

Fig. 7. Community metrics plotted against total catch. Evenness (*a*, *b*, *e*, *f*) and size diversity (*c*, *d*, *g*, *h*) for (*a*–*d*) Georges Bank (hundred kilotonnes) and (*e*–*h*) North Sea (megatonnes), for a given level of catch when size-selectivity is S- (*a*, *c*, *e*, *g*) or bell-shaped (*b*, *d*, *f*, *h*). Filled symbols, selective fishing; open symbols, nonselective fishing. Targets / bounds: diamonds, small; circles, medium; squares, large. For selectivity parameters see Table 3. Symbol size increases with maximum fishing mortality at the community level (from 0.2 for the smallest, to 1 for the largest symbols).

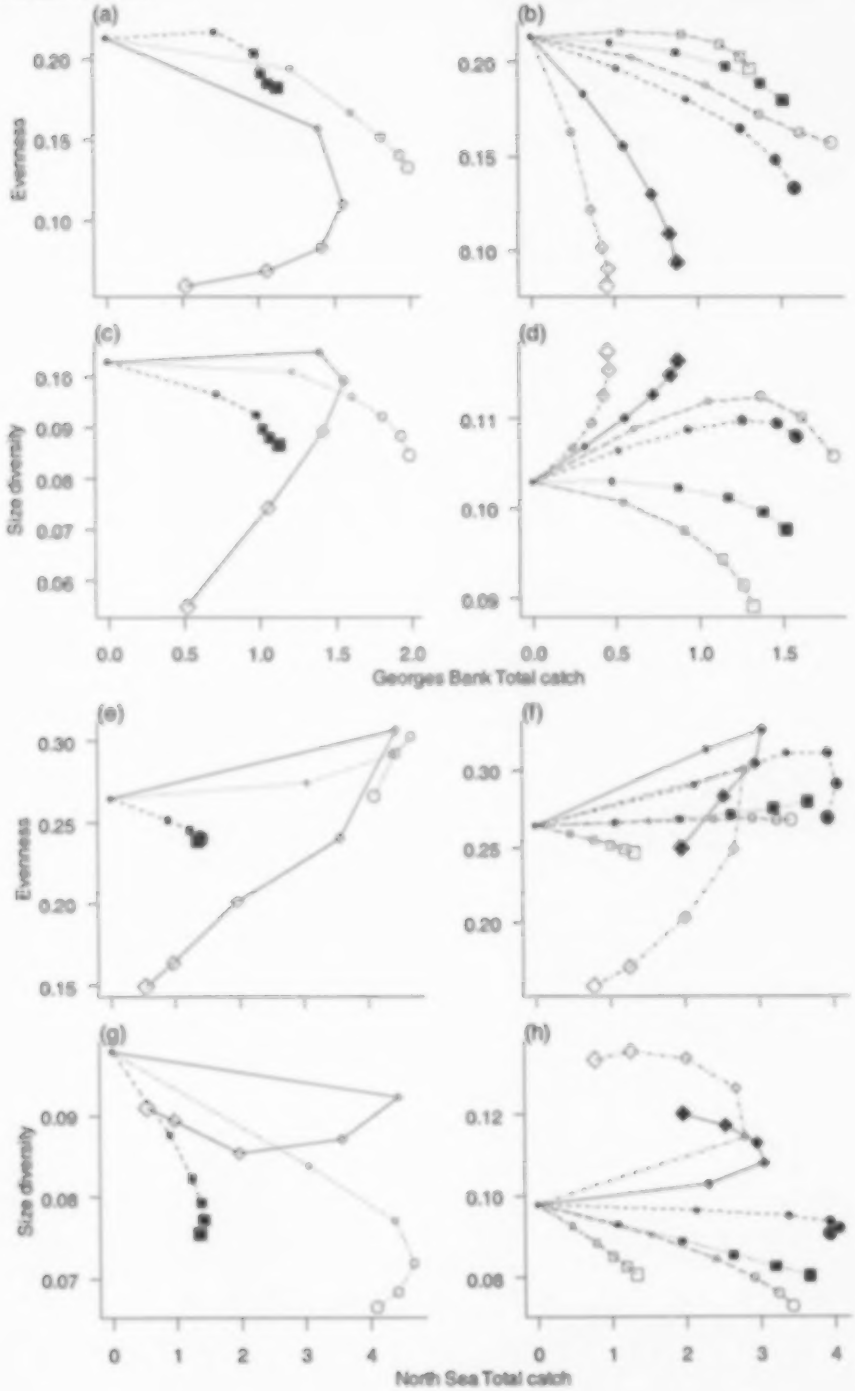
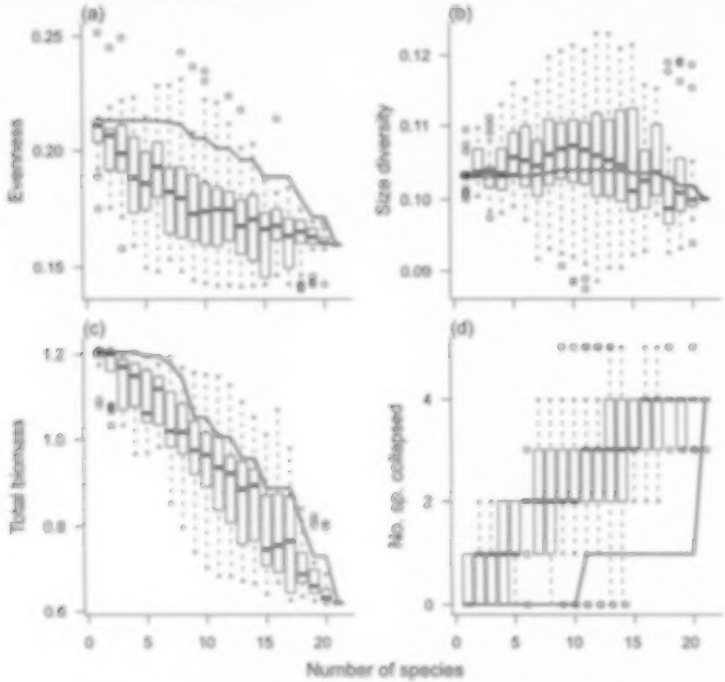


Fig. 8. Distribution of community metrics for Georges Bank versus number of species fished, where the target set is selected randomly, for $F_{full} = 0.4$. The bold line is the reference level for nonselective fishing, that is, the level of the metric that would be reached when catching the same amount (total catch mass) if all species were targeted. Box, interquartile range; bold line, median. (*a*) Evenness, (*b*) size diversity, (*c*) total biomass in megatonnes, (*d*) number of species collapsed.



with a bell-shaped curve targeting medium-sized fish, selectively in the North Sea and unselectively on Georges Bank.

Species selectivity

When including the Georges Bank species randomly in the target set, diversity metrics decreased as the number of species fished increased (Fig. 8). Total catch increased monotonically as the number of species targeted increased (not shown), and as a consequence, total biomass in the community decreased, but less steeply when fishing everything rather than a smaller target set (Fig. 8*c*). For a similar catch, species diversity metrics were always higher when fishing nonselectively for all species rather than any set. Both evenness and the number of species collapsed seemed to be relatively insensitive to nonselective fishing up to catches of 150 000 tonnes (that is, 12.5% of total biomass in the unfished system, corresponding to subset of up to 10 species), but responded monotonically when fishing selectively (Figs. 8*a* and 8*d*). Size diversity was relatively insensitive to non-selective fishing, and slightly increased when targeting small subsets up to 13 species, but the difference was small compared with sampling variability (Fig. 8*b*).

The general pattern was similar in the North Sea, with the following differences (Fig. 9). (*i*) When all species were fished, the reference line showed that evenness in the community increased with total catch (because the most abundant species, sandeel and herring, were increasingly depleted). In contrast, evenness was a U-shaped function of the number of species targeted. (*ii*) Only one species was collapsed at $F_{full} = 0.4$ in the North Sea. With $F_{full} = 0.8$ (not shown), the pattern was similar to Georges Bank, thereby illustrating that nonselective fishing had a lower impact than selective fishing. (*iii*) Size diversity decreased with total catch, and was always higher when fishing everything than when targeting a smaller set. Again, using total value of catch rather than mass to calculate the reference level produced very similar figures (not shown).

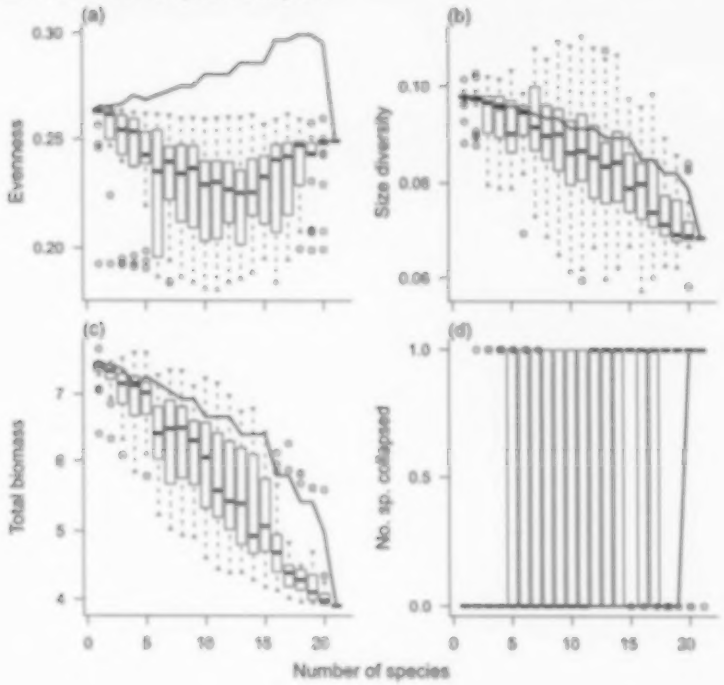
Discussion

Does selective fishing conserve community biodiversity?

Fishing all species unselectively had smaller effects on the selected biodiversity metrics for the community than selectively targeting a restricted set of species, and selectively fishing large fish did not maximize biodiversity for a given level of catch mass or value. Moreover, the differential effects of fishing selectivity are larger when fishing intensity is high. The effects of size-selectivity on species- and size-diversity depended on (*i*) the shape of the size-selection curve, and (*ii*) the community size-structure and species composition. Our results are also conditional on the choice of diversity metrics and on adopting total catch as a measure of fishing pressure on the community.

The predicted effects of size-selectivity and target size depended on whether the size-selection curve was S- or bell-shaped. The direction of effects and the selectivity that maximized each given metric differed among selection curves. Given the variety of predicted responses, which of

Fig. 9. Distribution of community metrics for North Sea versus number of species fished, where the target set is selected randomly, for $F_{full} = 0.4$. The bold line is the reference level for unselective fishing, that is, the level of the metric that would be reached when catching the same amount (total catch mass) if all species were targeted. Box, interquartile range; bold line, median. (*a*) Evenness, (*b*) size diversity, (*c*) total biomass in megatonnes, (*d*) number of species collapsed.



the size-selection models is likely to be more realistic? These models should describe, across all species, the proportion of the available fish in each size-class that are caught. As we are focusing on multigear, multispecies fisheries, this proportion is not easy to determine, since the selection curves will differ among gears and species. Fishing mortality estimates from stock assessments suggest that selectivity curves for most species are S-shaped on Georges Bank and bell-shaped in the North Sea, although this seems counterintuitive because these species are caught mainly by trawl. However, fishing mortality at age (or length) might not be a good proxy for selectivity when large individuals are scarce in catch statistics. As there are few, if any, fish in the oldest age classes, they are often collapsed in a "+ group" in assessment models, and changes in fishing mortality in the largest size classes are not estimated. While we consider that the stock assessment results were the best available information to check that theoretical selection curves were correctly parameterized, they cannot be used to determine which curve is most appropriate. As a sum of species size-selection curves, the community size-selection curve would be S-shaped on Georges Bank, and a rather wide bell in the North Sea. Unfortunately these estimates were available for only a subset of the species in the model, which are themselves a small subset of the species in the actual communities. Field studies are needed to improve our knowledge of selectivity at the community scale. Obviously they will be complicated by the difficulty of obtaining a reliable estimate of the species and size classes available, and when several gears are used and each one catches a different part of a population or community, no one gear is likely to give a complete picture (e.g., Bellchambers and de Lestang 2005; Olin et al. 2009). Novel work is required in this field, and for now, results with both selection curves are retained.

Modeling communities

The predicted effects of fishing selectively were different on Georges Bank and in the North Sea. These differences can be ascribed to differences between the modeled or the actual communities, and raises the question of how well the model captures the properties of the real communities.

Species evenness was higher in the North Sea because of a less steep slope of species dominance. The North Sea did not lose species as quickly, even with high fishing mortality, possibly because more of the North Sea is dominated by small- and intermediate-sized species with correspondingly higher growth and reproductive rates. In contrast, intermediate- and large-sized species dominated on Georges Bank, and size diversity and average mass were higher, consistent with the biomass spectrum peaking at larger sizes. Differences in the modeled fish communities arise from the input life-history parameters and influence the response to selective fishing. With no fishing, the biomass spectrum for Georges Bank peaks at 70–80 cm, with a subpeak at 40–50 cm, reflecting the dominance of haddock. In contrast, the unfished North Sea biomass spectrum peaks at

20–30 cm, with a subpeak at 60–70 cm. This difference, which is generated by the distribution of biomass among species, determines the outcome of size-selective fishing.

The two refinements made to the LeMANS model improved its stability and realism. Increasing the preferred prey:predator mass ratio (μ) and breadth of the size-preference function (σ) helped to stabilize the model dynamics, as would be expected from other studies (e.g., Benoît and Rochet 2004; Emmerson and Raffaelli 2004). It also reduced the predation mortality on the smallest size class, because it became less vulnerable to intermediate-size predators, which have high biomass. The smallest size-class is particularly vulnerable to the effects of predation, because individuals grow out of it relatively quickly and it is only replenished by recruitment at the end of each year. The inclusion of an explicit forage species provided additional biomass in the smallest size classes. An advantage of this formulation is that the abundance of forage species is now dynamically linked to predator abundance (Gislason 1999) and it can be compared with empirical estimates of available food. The magnitude of maximum spawning stock biomass S_{max} assumed for the forage species is consistent with the amounts of plankton and benthos available to fish, as estimated with food-web models (Collie et al. 2009; Mackinson and Daskalov 2007). Assuming a production-to-biomass ratio of approximately 1, we estimated similar densities of plankton and benthos biomass on Georges Bank (189 g·m^{-2}) and the North Sea (159 g·m^{-2}). Scaling these densities by area gives a total biomass of plankton and benthos of 7.34 Mt on Georges Bank and 90.63 Mt in the North Sea; values that exceed the assumed S_{max} of, 5 and 50 Mt, respectively, and the equilibrium biomass with no fishing of 4.2 Mt and 22.9 Mt. The difference can be ascribed to not all the plankton and benthos being a suitable size for fish prey, and plankton and benthos having a lower energy content than fish (Dauvin and Joncourt 1989; Pedersen and Hislop 2001), such that a greater mass of invertebrates is required to satisfy the consumption of the fish species. Therefore the assumed biomass of forage species is not excessive.

Being satisfied with the predictions of selectivity impacts on two example communities, we now can ask how general these results are, and to what extent they can be generalized to other communities. Using a size spectrum model, Rochet et al. (2009) found that fishing selectively decreases size diversity more than fishing less selectively. Andersen and Pedersen (2010) developed a size- and trait-based model in which life-history is scaled by asymptotic length, and predation is governed by length; they found that targeting all life-histories would remove large fish, while targeting more restricted sets of asymptotic lengths would create peaks and valleys in the size-spectrum. That we did not find such general results of the effects of size-selective fishing in the present study can probably be ascribed to the size-spectra being less regular here, which might be a more realistic description of actual size-spectra. Impacts of size-selectivity depend on the overlap between the size-selection curve and the community size-spectrum. The size spectrum will be depleted where it overlaps with the size-selection curve, and some top-down cascade might occur when fishing and biomass co-occur at medium to large sizes. Depending on the shape of the "unfished" size-spectrum, it can be inferred how fishing selectivity will either improve its regularity (by depleting peaks), thus increasing size diversity, or decrease its slope and (or) create additional crests or valleys, thereby decreasing size diversity.

The effects on species diversity, however, depend on the species composition and size-range of each species. The result that selectively fishing large fish does not maximize biodiversity for a given level of catch is probably valid across a wide range of communities. A community that would not be impacted by the selective removal of the largest individuals would be either one with a peak in large sizes (which is unusual, as size spectra are generally decreasing, Kerr and Dickie 2001); or one with no fish at all in the large sizes, but in that case selectively fishing large fish would not yield anything. As for the result that fishing all species evenly affects biodiversity less than selectively targeting a restricted set of species, the pattern was consistent across the two communities and two fishing intensities (F_{full} = 0.4 and F_{full} = 0.8). It is likely that targeting a particular combination of species with similar size-ranges and (or) high dominance would affect biodiversity in a different way; however, as we focused on species selectivity, that is, the number of species, and constructed random sets, these particular sets were diluted among all other sets of species. Thus it is probable that our species selection findings are quite general.

Measuring biodiversity and fishing pressure

These results are largely determined by the way we standardized fishing pressure across fishing scenarios, and by our choice of biodiversity measures. A simple measure of fishing pressure on an entire community is difficult to find. Average fishing mortality rate F across species has been used in empirical analyses (e.g., Blanchard et al. 2005), and is roughly equivalent to the maximum fishing mortality rate in the present study. However, it cannot be used to compare the effects of different selectivity options; just as fishing mortality rates in single-stock models are comparable only for a given exploitation pattern. Our choice of total catch provides one measure of the ecosystem service provided by fisheries in units of the amount of food provided. This measure is appropriate if we consider that one objective of fisheries management is to maximize yield, under sustainability constraints. However, in fisheries that are not exploited solely to maximize food supply, the composition and value of the catch may be more important objectives, and greater weighting may be given to larger and higher value species than smaller forage fish. Remarkably, the results of our alternate analyses that measured fishing pressure in units of total catch and total value were relatively consistent, despite >10-fold differences in the price of fishes sold for reduction and direct human consumption.

In the context of assessing the ecosystem effects of fishing, which is the main focus of this analysis, total catch may not be an equitable measure of fishing pressure on the community, since the impact of a given catch of smaller species and size classes, where production and biomass are high, will be lower than the impact when the same catch is removed from larger size classes, where production and biomass are lower. A differential weighting of size-classes would then be appropriate. We expected that using catch value instead of mass would account for this, but because

price data were not size-dependent within species, such a relationship was not apparent.

The choice of biodiversity metric, even if explicitly specified as a management objective, still requires a value decision. Our choice of two species diversity indices describing richness and evenness independently solves the balance between these two components implied by most combined indices (Magurran 2004). As expected, the effects of fishing selectivity were not the same on these two facets of biodiversity. Nonselective fishing did not always result in the highest rate of species "collapses", while evenness was generally higher with unselective fishing. As for size diversity, our index values even size distributions with more weight given to large fish; we acknowledge that this weighting is arbitrary and that different indices would lead to different conclusions. Attempts to assess the effects of different management actions on progress towards an objective will always require that the objective is explicitly defined. Remarkably, few explicit objectives for biodiversity exist despite statements that high biodiversity is "good" and high-level political aspirations to conserve biodiversity (Greenstreet 2008). In practice, the few existing and explicit management objectives for biodiversity focus on the protection of rare and vulnerable species and habitats.

How selectively should we harvest our oceans?

So, should we think technologically, as heirs of a single-stock management perspective, and improve selectivity to reduce by-catch and protect biodiversity? Or should we think ecologically, and considering fishing impacts on the community level, fish evenly to preserve ecosystem structure and function? The latter idea is not new. For example, Caddy and Sharp (1986) proposed a "utopian" exploitation strategy, which consisted of fishing each species in proportion to the rate of natural predation it is subjected to; more recently Fowler (1999) similarly suggested determining exploitation rates based on consumption rates by natural predators. In the same vein, Larkin (1977) conjectured that a preferable technique of harvesting ecosystems would be to take the same proportion of everything above a certain size. Fogarty and Murawski (1998) thought that this type of broad harvesting pattern at low exploitation rates would entail a lower risk of altering ecosystem structure. Based on literature review of fishing impacts on tropical reef ecosystems, Jennings and Polunin (1996) suggested that harvesting a range of animals from various trophic groups might produce high yields without initiating ecosystem shifts. Besides these broad intuitions, is more accurate theory or empirical evidence available?

It seems difficult to provide a general answer to the question. While a size-spectrum model (Rochet et al. 2009) showed that selectively fishing large fish might jeopardize the system stability and decrease its size diversity, the present study suggests that the actual effects of size-selectivity will depend on the overlap between the selection curve and initial size-spectrum in the community, that is, on the particular combination of gear selectivity, fishing intensity, and ecological settings in a given fishery. As for species selectivity, the general answer provided here that wide target sets are more conservative than narrower ones, might be of little practical application. A given type of fishing gear will selectively catch species with similar behavior, which may consequently have related ecological functions; thus, not all species subsets are equally probable, and the random selection of fixed-size subsets may be too vague an approach to this problem.

A general answer might be of little use and more detailed, system-specific studies may be required. However, the results of such studies still very much depend on their choice of the measure of impact at the community or ecosystem level and the relationships between fished species and other components of the ecosystem. For example, McClanahan (1995) developed a coral reef ecosystem model to investigate the effects of various fishing patterns on yields, production and coral growth. He found that fishing everything would reduce total yield at low fishing intensity, while targeting only piscivores would prevent high yields; only a strategy targeting both piscivores and herbivores but avoiding invertebrate feeders preserved high yields, high productivity, and biodiversity. Other studies have used mass-balance models: Bundy et al. (2005), starting from the assumption that balanced exploitation would minimize ecosystem disturbance, used an index that measured the impact on relative biomass at different trophic levels. For the Gulf of Thailand fishery, they found that the highest impact resulted from the heavy exploitation of high trophic levels and the lowest from targeting low trophic levels, while the impact of balanced exploitation would be intermediate. In a Mediterranean trawl fishery Coll et al. (2008) found that total system biomass was insensitive to improved gear selectivity, while a biodiversity index (including only high trophic level species) would increase. There is no general answer from these system-specific studies.

There is little evidence of the effects of changing fishing selectivity from field studies. Bundy et al. (2005) found that the changes in exploitation balance and intensity on the eastern Scotian Shelf between 1970 and 2002 did not have the expected effects on an ecosystem disturbance index predicted by a mass-balance model and ascribed this to lag effects and environmental changes. Increasingly, gear-trial type studies describe the diversity of the catch and other multispecies metrics while comparing gears or mesh sizes. However, this amounts to describing the pressure exerted by various gears on the community. As for the resulting impact, both nonselective and selective fishing practices were found to be capable of modifying the structure of reef fish populations in a visual census comparison of 36 fishing grounds (Campbell and Pardede 2006). More studies that combine accurate assessments of both pressure and the structure of the community are needed.

Using a wide diversity of gears might be the way towards more balanced exploitation patterns (Bundy and Pauly 2001; Misund et al. 2002); since a variety of fisheries each selectively taking their preferred target species might, on aggregate, fish most parts of the food web. Alternatively, when unselective gears are used, by-catches are not necessarily harmful; but the use of those species that currently lack commercial value might be encouraged to minimize discarding (Clucas 1997). The model here did not consider how the recycling of discarded by-catch in the food-web might mitigate the effects of removals. Finally, little is known about what fishing gears select out of a community. Although

predicted effects were highly dependent on the shape of the selection curve, we are ignorant of which one would be more appropriate in which circumstances. For the development of an ecosystem approach to fisheries, including exploitation strategies at the community scale, we need to expand our knowledge in this field.

In conclusion, what is our answer to the question of which fishing selectivity pattern best conserves community biodiversity? Certainly the general statement that improving selectivity will protect biodiversity cannot be taken for granted, unless the focus of biodiversity conservation is solely on the status of a few rare or vulnerable species that can be avoided by improved selectivity. But the alternate statement that nonselective fishing conserves biodiversity better is *not* necessarily true either. Our analysis shows that any structured debate to inform management will need to be based on clear definitions of biodiversity, and knowledge of the management objectives for biodiversity and the fishery.

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Modeling the response time of diatom assemblages to simulated water quality improvement and degradation in running waters

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Abstract: The objective of this study was to measure and model the response time of the Eastern Canadian Diatom Index (IDEC: Indice Diatomées de l'Est du Canada), a diatom-based index of biological integrity, following substrate translocation from altered sites (nutrient-enriched) to pristine sites and vice-versa. The frequency of sampling, duration (time after substrate translocation), and variety of site conditions in the present study provide strong evidence for an accelerated response of diatoms to a degradation reflecting eutrophication (within a week in certain cases) and a slower path to recovery (up to 4 weeks). Diatom response varied as a function of trophic status; oligotrophic rivers responded rapidly to a degradation, and mesotrophic or eutrophic rivers responded more slowly to an amelioration of the conditions. Variation in response time as a function of trophic status seemed to be partly linked to the diversity and complexity of the assemblages. The less diverse assemblages observed in oligotrophic waters were highly sensitive to nutrient enrichment, whereas the more diverse assemblages sampled in mesotrophic–eutrophic rivers were less sensitive to nutrient fluctuations, and major variations in nutrient concentrations took a longer time to induce a change in index values.

Résumé : L'objectif de notre recherche est de mesurer et de modéliser le temps de réaction de l'Indice Diatomées de l'Est du Canada (IDEC), un indice d'intégrité biologique basé sur les diatomées, à la suite d'un déplacement de substrats de sites altérés (enrichis en nutriments) vers des sites vierges et vice-versa. La fréquence de l'échantillonnage, la durée (temps écoulé depuis le déplacement des substrats) et la variété des conditions dans les sites de notre étude permettent d'obtenir des données probantes qui montrent une réaction accélérée des diatomées à une dégradation qui représente une eutrophisation (en moins d'une semaine, dans certains cas) et une voie de récupération plus lente (jusqu'à 4 semaines). La réaction des diatomées varie en fonction du statut trophique : les rivières oligotrophes réagissent rapidement à une dégradation, alors que les rivières mésotrophes ou eutrophes réagissent plus lentement à une amélioration des conditions. La variation du temps de réaction en fonction du statut trophique semble être reliée en partie à la diversité et la complexité des peuplements. Les peuplements moins diversifiés observés dans les eaux oligotrophes sont très sensibles à l'enrichissement par les nutriments, alors que les peuplements plus diversifiés échantillonnés dans les rivières mésotrophes–eutrophes sont moins sensibles aux fluctuations des nutriments; les variations majeurs dans les concentrations de nutriments mettent donc plus de temps à provoquer un changement dans les valeurs de l'indice.

[Traduit par la Rédaction]

Introduction

Diatoms are used in an increasing number of countries as an effective tool for monitoring the biological integrity and the water quality of water bodies. These microscopic algae are present in all aquatic ecosystems and are sensitive to variations in their environment (e.g., changes in nutrient concentrations, conductivity, pH, temperature), which makes them good indicators of anthropogenic stresses such as eutrophication (Kelly and Whitton 1995; Hall and Smol 1999). Diatom assemblages, characterized by a high diversity of taxa, yield ecological information that allows for the development of biological indices based on robust statistical analyses. Numerous diatom-based indices have been developed in various countries and are integrated into water quality monitoring programs as an additional tool for assessing ecosystem health (Coste 1982; Kelly and Whitton 1995; Prygiel and Coste 2000). In Canada, the Eastern Canadian Diatom Index (IDEC: Indice Diatomées de l'Est du Canada) was created for monitoring river eutrophication (Grenier et al. 2006; Lavoie et al. 2006*a*, 2008*a*) and has been used to

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assess the biological integrity of more than 100 streams and rivers to date (more than 1000 sites).

Diatoms integrate variations in nutrient concentrations over short periods (Lavoie et al. 2008*a*). Diatom indices are therefore complementary to invertebrate and fish indices, which integrate water and habitat quality over longer time periods (Karr and Chu 1999). However, only a few studies show evidence of the integrating potential of diatom assemblages. These studies are based on two approaches: the first consists of the evaluation of the correlation between diatom index values and environmental variables, whereas the second approach is based on the translocation of artificial substrates.

In the first approach, diatom index values (calculated from species relative abundances) are commonly correlated with water chemistry values averaged over various time periods (e.g., weekly, monthly). A study conducted by Taylor et al. (2007) suggested that diatom-based indices in general (numerous European indices were tested) have the best correlation with chemical data averaged over 1 month, starting 6 weeks before diatom sampling. Based on a similar approach using the IDEC, Lavoie et al. (2008*a*) suggested that the integration period varies with trophic status and nutrient concentration variability in the rivers. In an oligotrophic river, where nutrient concentrations were low and generally stable, they found that a natural increase of phosphorus induced a rapid change in diatom assemblage structure and IDEC value within 1 week. In a mesotrophic river, the observed integration period was approximately 2 weeks. Diatom assemblages in a eutrophic river appeared to be adapted to frequent and substantial fluctuations in nutrient concentrations, with a 5-week integration indicating a slower response to short-term fluctuations. These two studies allowed for the evaluation of the ability of diatom indices to integrate temporal variations in environmental parameters, but did not provide direct information on the response time following a degradation or an amelioration in environmental conditions.

In the second approach, artificial substrates are translocated, following a colonization period, from a polluted site to a reference site and vice-versa to measure the response time of diatom assemblages and indices. This approach has been used in a wide range of environments in several studies (e.g., Gold et al. 2002; Tolcach and Gómez 2002; Rimet et al. 2005). These studies show that diatom assemblages have a shorter response time following a degradation than following an amelioration of environmental conditions. In addition, substrate translocation simulating a sudden degradation in water quality is generally accompanied by a decrease in the number of pollution-sensitive taxa and an increase in the number of pollution-tolerant taxa. These studies provide information related to the structural modifications in diatom assemblages and the response time of indices following a change in water quality. However, there are still aspects that need further investigation: (*i*) Few studies have measured the changes in assemblages shortly after the translocation of the substrates. The short life cycle of diatoms may allow for a rapid (within a week) response of assemblages and indices. (*ii*) The time frame of the translocation studies is often inadequate to evaluate the period of time needed for a complete recovery (or degradation) of the diatom assemblages. (*iii*) The sampling frequency following substrate translocation is often too low to observe gradual changes in diatom assemblages or to determine the actual response time. (*iv*) Past studies suggest that the response time of diatom assemblages and indices may vary as a function of the pH and the trophic status of the ecosystem (Lavoie et al. 2008*a*), but these relationships have not been explored systematically. (*v*) No experimental studies have been conducted to determine the response time of the IDEC.

The objective of our study was to measure and model the response time of the diatom-based index IDEC following substrate translocation from nutrient-enriched sites (altered) to pristine sites and vice-versa. The sampling design of the present study allowed us to address the issues listed above, thus providing a more complete examination of the effects of translocation on diatom assemblages than has been achieved to date.

Materials and methods

Site selection and diatom sampling

Five pairs of rivers located in eastern Canada (Quebec) were selected to simultaneously study the response time of the IDEC following a degradation (increase in nutrient concentrations) and an amelioration of water quality (decrease in nutrient concentrations). Based on IDEC values previously calculated for these sites (Lavoie et al. 2006*a*), five rivers were representative of reference or least-impacted conditions (oligotrophic–mesotrophic) and five rivers were representative of altered conditions (mesotrophic–eutrophic). Each pair of rivers included an altered site and its specific reference site. The selected reference or least-impacted site for each pair belonged to the same ecophysiographic group as the altered site, as established in Grenier et al. (2006). Among the five pairs of rivers selected, three had naturally lower pH levels (the reference sites had a water pH naturally slightly acidic to neutral) and two were located in more alkaline environments (the reference sites had slightly alkaline water pH). The distinction between the rivers as a function of their pH at reference state (based on their geological characteristics) was necessary to determine which IDEC subindex to use (IDEC-Neutral or IDEC-Alkaline; Grenier et al. 2006).

The pairs of rivers selected for each subindex, as well as their IDEC values (data from 2003; Lavoie et al. 2006*a*) are presented (Table 1), as well as physical and chemical characteristics of each river (Table 2). Based on the nutrient criteria, the 10 study sites were grouped as a function of their trophic status using long-term data from the Ministry of the Environment of Quebec: Ste. Anne and Noire rivers are oligotrophic (total phosphorus, TP: <25 $\mu g \cdot L^{-1}$; total nitrogen, TN: <700 $\mu g \cdot L^{-1}$; Dodds et al. 1998); Shawinigan upstream, Nicolet, Des Envies, Yamaska Sud-Est, and Yamaska rivers are mesotrophic (TP: 25–75 $\mu g \cdot L^{-1}$; TN: 700–1500 $\mu g \cdot L^{-1}$; Dodds et al. 1998); and Shawinigan downstream, Nicolet Sud-Ouest and Blanche rivers are eutrophic (TP: >75 $\mu g \cdot L^{-1}$; TN: >1500 $\mu g \cdot L^{-1}$; Dodds et al. 1998).

Six concrete blocks (19 cm × 19 cm × 39 cm) were placed in each of the 10 rivers in mid-June 2006. Six nonglazed ceramic tiles (25 cm^2) were mounted on each block using plastic-coated wire. Each tile corresponded to a sam-

Table 1. Pairs of reference and altered streams with their IDEC values in circumneutral and alkaline conditions.

IDEC-Neutral						IDEC-Alkaline			
Pair 1		Pair 2		Pair 3		Pair 4		Pair 5	
IDEC	River	IDEC	River	IDEC	River	IDEC	River	IDEC	River
100	Noire	79	Shawinigan (upstream)	93	Ste. Anne	100	Yamaska Sud-Est	50	Nicolet
0	Blanche	28	Shawinigan (downstream)	19	Des Envies	23	Yamaska	19	Nicolet Sud-Ouest

Note: River status (reference or altered) and IDEC values are derived from Grenier et al. (2006) and Lavoie et al. (2006*a*).

pling period, i.e., time 0 was before translocation, the remaining five tiles corresponded to 1, 2, 4, 8, and 12 weeks following the translocation. The artificial substrates were incubated in situ for a period of 4 weeks before being translocated to allow for colonization of the tiles by the periphytic assemblages. After the 4-week incubation period, diatom assemblages were sampled from the time 0 tiles. Three blocks from each river (i.e., half of the substrates) were then translocated to the opposite environment (i.e., tiles from reference sites were moved to altered sites and vice versa). During transportation, the blocks were placed in large containers filled with 2 cm of river water (to keep moisture in the container), and the tiles were covered with a plastic film to avoid desiccation of the biofilm. No substrates were kept in the containers for more than 45 min. The blocks that were not translocated were also placed in containers and transported before returning to their initial location to ensure that these assemblages were exposed to the same stress as the translocated assemblages.

Diatom sampling was performed following the recommendations in Kelly et al. (1998) and the procedure described in Lavoie et al. (2006*a*) for the development of the IDEC. Periphyton was scraped off the tiles using a toothbrush, and the samples were preserved with Lugol's solution. The samples were digested in 30% hydrogen peroxide to remove cell content (to facilitate taxonomic identification) and were mounted on microscope slides using Naphrax. A total of 400 valves per slide were counted and identified at a 1000× magnification. The identification of the diatom taxa was performed using a diatom guide created for use with the IDEC (Lavoie et al. 2008*b*). The Shannon's diversity index was calculated for each sample collected during this study.

IDEC calculation

IDEC values are calculated based on the relative abundance of diatom taxa (Lavoie et al. 2006*b*) and reflect changes in the structure of assemblages such as a progressive increase in tolerant taxa following a degradation of the environment (mostly reflecting an alteration due to eutrophication). The IDEC was developed based on a correspondence analysis (CA) to evaluate the position of sites along the gradient of maximum variation (first ordination axis). The IDEC gradient ranges between 0 and 100, and the index value indicates the distance of an altered diatom assemblage from its specific reference assemblage. A high index value represents a non- or least-altered site, while a low index value represents a more heavily altered site. To account for ecoregion characteristics and natural pH variations, two sub-indices were created based on the two major groups of diatom reference assemblages observed: the IDEC-Neutral includes the sites that have reference assemblages characteristic of slightly acidic or neutral water pH, whereas the IDEC-Alkaline includes the sites that have reference assemblages characteristic of environments where pH values are naturally slightly alkaline. A detailed explanation of the methodology used to determine the reference diatom assemblages is presented in Grenier et al. (2006). Since the completion of the present study, a new version of the IDEC (IDEC 2.0; Lavoie et al. 2010) was created including samples from Ontario and the Maritimes. This new version provides a better representation of environmental conditions found in eastern Canada. However, the new version of the IDEC was not available for this study on substrate translocation.

Piecewise regression models

Differences in the IDEC value between the translocated substrates and the in situ substrates that remained at the hosting site (ΔIDEC) were calculated for each of the six sampling periods (time 0 (immediately before transfer) and weeks 1, 2, 4, 8, and 12 after translocation) and plotted. The response of the ΔIDEC in the period following substrate translocation clearly suggested a two-phase pattern in the diatom assemblage turnover. The initial phase was characterized by a rapid change in the structure of the assemblages, whereas the second phase showed a stabilization in the rate of assemblage change, as revealed by the ΔIDEC. Piecewise regressions were therefore chosen to model the response of the ΔIDEC. When the ΔIDEC stabilizes at a value near zero, the breakpoint time (c), at which the regression line for the first phase intersects the regression line for the second phase, indicates the time at which the translocated and in situ assemblages have converged in structure. Two different piecewise regression models were used to represent the time course of the ΔIDEC: the first (and simpler) of the two models, M1, represents the two phases with separate regression lines that intersect at breakpoint time c, with the slope of the regression set to zero for time > c. This constraint on the second slope reflects an assumption of no further change in the ΔIDEC after time c. The second model, M2, also represents the two phases with separate regressions that intersect at time c, but has no restriction on the slope for time > c. This model assumes that the rate of change in ΔIDEC undergoes a transition at time c, but does not assume that the ΔIDEC stabilizes completely after time c. For both models, the slope prior to convergence measures the initial rate of convergence (negative slope coefficient) or, potentially, divergence (positive slope coefficient) between

Table 2. Mean values for water chemistry variables from January to December 2006.

	Noire	Blanche	Shawinigan upstream	Shawinigan downstream	Ste. Anne	Des Envies	Yamaska Sud-Est	Yamaska	Nicolet	Nicolet Sud-Ouest
Total phosphorus (μg·L^{-1})	9	96	23	100	16	37	22	38	34	91
Total nitrogen (μg·L^{-1})	236	860	260	778	235	731	438	585	1308	1099
Ammonia (μg·L^{-1})	22	33	30	330	20	70	18	76	35	95
Dissolved organic carbon (mg·L^{-1})	5.8	5.5	4.6	7.7	3.9	6.7	4.2	6.1	7.8	10.4
Chlorophyll *a* (mg·m^{-3})	2.08	6.75	NA	3.39	1.77	4.65	2.01	8.34	6.70	9.05
Coliforms (CFU, 100·mL^{-1})	9	246	NA	3638	14	233	126	403	914	203
Conductivity (μS·cm^{-1})	16.1	82.7	22	141.8	21.6	81.5	86.0	165.8	218.7	216.4
pH	5.8	7.2	6.8	7.0	6.0	7.0	7.2	7.4	7.6	7.7
Suspended solids (mg·L^{-1})	2	60	NA	7	5	11	10	12	13	95
Turbidity (NTU)	1.0	30.9	NA	6.5	2.2	14.3	4.0	5.7	5.0	39.4
Water temperature (°C)	9.5	9.7	NA	10.5	10.0	10.5	10.5	9.2	10.9	12.0
Salinoles	IDEC-Neutral	IDEC-Neutral	IDEC-Neutral	IDEC-Neutral	IDEC-Neutral	IDEC-Neutral	IDEC-Alkaline	IDEC-Alkaline	IDEC-Alkaline	IDEC-Alkaline
Trophic category	Oligotroph	Eutroph	Oligotroph	Eutroph	Oligotroph	Mesotroph	Oligotroph	Mesotroph	Mesotroph	Eutroph

Note: CFU, colony-forming unit; NTU, nephelometric turbidity unit; NA, not available. The trophic categories are based on Dodds et al. (1998) using long-term data from the Ministry of the Environment of Québec, data from the Ministry of the Environment, Québec.

two assemblages. An F test was used to determine whether the additional complexity of M2 provided an improvement in fit over M1, i.e., whether the slope for the second phase was statistically indistinguishable from zero as assumed by M1. The F statistic was calculated as

$$F_{p-q,n-p} = \frac{(\mathrm{RSS}_1 - \mathrm{RSS}_2)/(p-q)}{\mathrm{RSS}_2/(n-p)}$$

where RSS_i is the residual sum of squares for model i (1 or 2), q is the number of parameters for M1 (3), p is the number of parameters for M2 (4), and n is the sample size. A major advantage of piecewise regression over many previous approaches to ecological degradation and recovery is that it yields not only point estimates of response times, but also measures of uncertainty about these estimates in the form of confidence intervals. Piecewise regression has been used previously to identify transition points in the response of species or ecological processes (Toms and Lesperance 2003) and between phases characterizing particle movement in a lotic ecosystem (Ryan et al. 2002). Piecewise regressions were performed using SYSTAT version 11 (Systat Software Inc., 2004).

Results

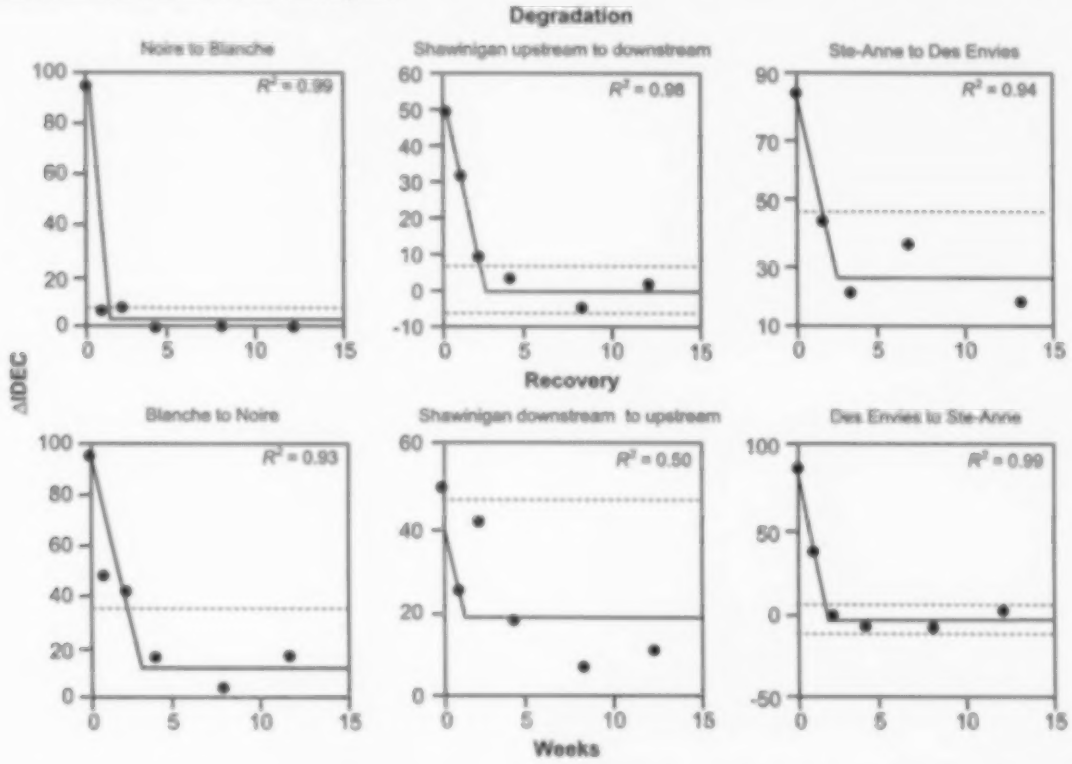
Diatom community structure and diversity

The diatom communities observed in the selected altered sites were different than what was observed in the pristine or least-impacted sites. In summary, nutrient-rich sites were colonized by species such as *Melosira varians*, *Nitzschia palea*, *Navicula capitatoradiata*, *Cocconeis placentula* var. *euglypta*, *Nitzschia amphibia*, *Navicula gregaria*, *Navicula germainii*, *Navicula tripunctata*, *Achnanthidium minutissimum*, *Nitzschia inconspicua*, and *Reimeria sinuata*. The species found in less-impacted sites included *A. minutissimum*, *Tabellaria flocculosa*, *Fragilaria capucina*, *Brachysira microcephela*, *Brachysira brebissonii*, *Staurosirella pinnata*, *Achnanthidium rivulare*, and various species of *Eunotia*.

The translocation of the substrates into their specific hosting site resulted in a drastic change in community structure. For example, the translocation of the assemblage from Noire River to Blanche River (degradation in naturally slightly acidic – neutral pH waters) resulted in a large drop in the relative abundance of *T. flocculosa* (43% to 1.5%), while *M. varians* (a species typical of polluted waters; Leland et al. 2001) increased from 0% to 28%. For the opposite translocation, the recovery simulated from Blanche River to Noire River resulted in a slower reorganization of the assemblage; *T. flocculosa* increased from 0% to 18.5% within 1 week. In naturally alkaline environments, the translocation from Yamaska Sud-Est River to Yamaska River (degradation) induced a large drop in *A. rivulare* (52% to 16% in 1 week) and an increase in *C. placentula* var. *euglypta* and *R. sinuata* (species typical of polluted waters; Rott et al. 1998; Krstic et al. 1999) from 0% to 32% within 2 weeks and 3% to 35.5% within 1 week, respectively. The change in diatom community structure after the 12 weeks of incubation in the hosting site is summarized in Appendix A, Table A1.

Average diversity values (Shannon's diversity index) for the different environmental conditions were calculated. Diversity

Fig. 1. IDEC-Neutral: piecewise regression showing the relationship between the differences in IDEC values (ΔIDEC) between the translocated blocks and the blocks that remained in situ and the number of weeks following substrate translocation in naturally circumneutral environments. Translocation from altered sites to reference sites (recovery) and vice-versa (degradation) is indicated. The dotted lines indicate the confidence interval for ΔIDEC after convergence.



was lower in environments with naturally slightly acidic to neutral water pH and oligotrophic conditions, in which assemblages were often dominated by *T. flocculosa* and *A. minutissimum*.

IDEC response time following translocation

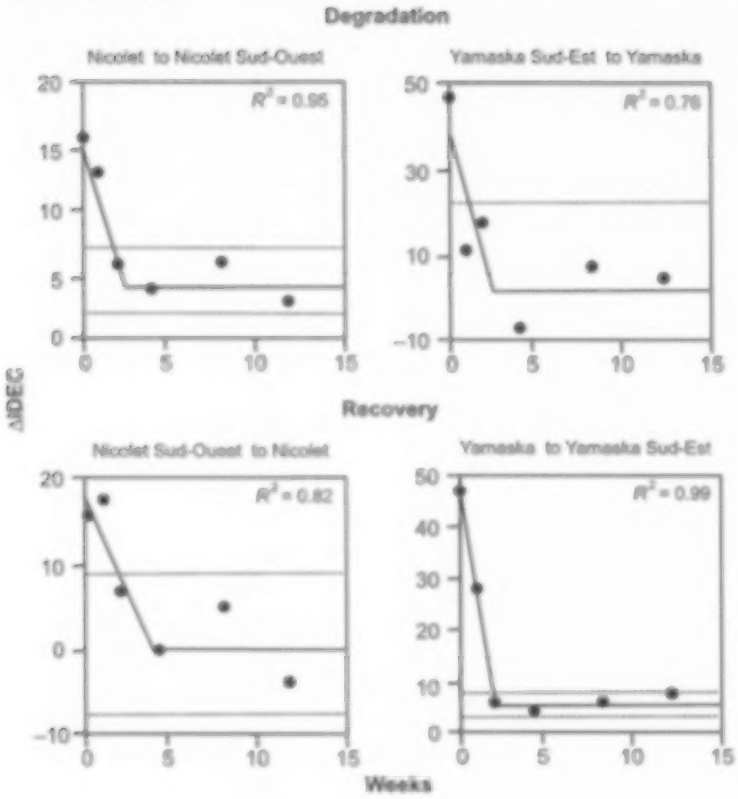
For the rivers with a naturally acidic to neutral water pH, translocation of the blocks from the Noire River (reference site) to the Blanche River (altered site) was followed by a rapid decrease in IDEC values (Fig. 1). At time 0, before the transfer, the IDEC values of these two sites were at opposite extremes of the pollution gradient (ΔIDEC = 97), near to the maximum gradient length of 100 units. Only 1 week after the translocation, the ΔIDEC had fallen to 6 units and the IDEC value of the translocated assemblage had nearly reached that at the hosting site. Four weeks after the translocation, the IDEC values had reached convergence. The changes observed for the translocation in the opposite direction were more gradual. One week after the transfer to the Noire River, the assemblage originating from the Blanche River started to converge, with a 49-unit difference from the host assemblage. After 12 weeks of incubation at the hosting site, the assemblage from the Blanche River was still different from the assemblage in the Noire River (ΔIDEC = 12). A similar pattern was observed in the Shawinigan River, where a rapid degradation (decrease in IDEC value) was observed within a 3-week period, while the recovery (increase in IDEC value) was more gradual. However, this trend was inverted in the case of the Ste. Anne and Des Envies rivers; the degradation of the assemblage in the Ste. Anne River was not completed after 12 weeks, while the assemblage in the Des Envies River had completely recovered after 2 weeks.

Rivers with a naturally alkaline pH showed less pronounced differences in IDEC values than rivers with a naturally slightly acidic to neutral pH (Fig. 2). This result was due to the reference conditions in naturally alkaline environments that are not true pristine conditions. Instead, the reference rivers represented the sites that were the least impacted (mesotrophic) and were selected for this study because of the difficulty of finding pristine conditions in the St. Lawrence Lowlands. Although the gradient in IDEC value (difference between reference or least-impacted sites and altered sites) was shorter in rivers with naturally alkaline pH, a similar pattern of change after translocation was observed in alkaline and acidic–neutral rivers. For example, the degradation and recovery of the assemblages from Nicolet River (mesotrophic) and Nicolet Sud-Ouest (eutrophic) were mostly completed within 4 weeks.

Modeling the response time

The comparisons of fit between M1 and M2 by means of

Fig. 2. IDEC-Alkaline: piecewise regression showing the relationship between the differences in IDEC values (ΔIDEC) between the translocated blocks and the blocks that remained in situ and the number of weeks following substrate translocation in naturally alkaline environments. Translocation from altered sites to reference sites (recovery) and vice-versa (degradation) is indicated. The dotted lines indicate the confidence interval for ΔIDEC after convergence.



F tests ($p > 0.08$ for all 10 comparisons of M1 and M2) indicated that it was reasonable to assume that the ΔIDEC stabilized after an initial phase of rapid change that preceded the breakpoint time c. Therefore, the emphasis hereafter is on the results of the piecewise regressions for M1 (Table 3; Figs. 1 and 2). Estimates of the slope of the postrecovery period (time > c) are based on few points, suggesting that statistical power was low in comparisons of M1 and M2. However, the consistency of results across trials ($p > 0.08$ for all 10 F tests comparing M1 and M2), as well as the apparent absence of a common postrecovery trend in ΔIDEC across trials (Figs. 1 and 2) provide little support for the more complex model M2.

The M1 model showed that the diatom communities and the IDEC values responded quickly to a translocation simulating a degradation of the environment (eutrophication). For example, the translocation of the diatom assemblages from Noire River to Blanche River (degradation) resulted in a response of the IDEC with an R^2 of 0.99. During the initial phase of the response, the IDEC value decreased at a rate of 91 units per week, which was the fastest rate observed during this study. Convergence occurred 1 week following the translocation, when the IDEC value of the translocated assemblage and the assemblage from the hosting site converged (at time c). The confidence intervals for c and for ΔIDEC after convergence are also presented (Table 3).

In the case of a recovery, IDEC values varied at a slower rate during the first phase of the response. For example, the tanslocation from Nicolet Sud-Ouest River to Nicolet River resulted in an average increase in IDEC value of 4.5 units per week during the course of the first phase. The convergence between the assemblages from the two rivers took 4 weeks and was therefore slower than the convergence associated with degradation.

The R^2 values presented (Table 3) are generally high, with the lowest value (0.50) observed for the recovery of the diatom assemblage in the Shawinigan River. The rate of change of IDEC values during the first phase of the response varied from 4.5 to 91 units per week. The rates of change during the first phase were faster in the environments with a naturally slightly acidic to neutral water pH (ranging from 20.5 to 91 units per week) than in the naturally alkaline environments (ranging from 4.5 to 21.5 units per week). Changes in IDEC values were also more rapid when the translocation simulated a degradation (ranging from 5 to 91 units per week) than when simulating an amelioration of the conditions (ranging from 4.5 to 49 units per week).

Table 3. Post-translocation rates of degradation and recovery for the 10 streams grouped according to their IDEC subindex.

	R^2	Rate of convergence (ΔIDEC per week)	Time to convergence (c, weeks)	Confidence interval for c	Confidence interval for ΔIDEC after convergence
Degradation					
IDEC-Neutral					
Noire to Blanche	0.99	91.0	1.0	0.9–1.2	–3.8–7.3
Shawinigan upstream to downstream	0.98	20.5	2.5	1.8–3.5	–7.0–8.4
Sainte-Anne to Des Envies	0.94	43.0	1.4	0.5–4.3	0.2–49.2
IDEC-Alkaline					
Nicolet to Nicolet Sud-Ouest	0.95	5.0	2.5	1.4–4.2	1.5–7.2
Yamaska Sud-Est to Yamaska	0.76	15.5	2.6	0.7–9.7	–21.1–23.1
Recovery					
IDEC-Neutral					
Blanche to Noire	0.93	27.5	2.8	1.4–5.7	–8.5–33.1
Shawinigan downstream to upstream	0.50	25.0	1.2	0.1–11.7	–5.7–45.7
Des Envies to Sainte-Anne	0.99	49.0	1.8	1.3–2.5	–9.8–4.3
IDEC-Alkaline					
Nicolet Sud-Ouest to Nicolet	0.82	4.5	4.0	0.6–27.1	–8.5–9.1
Yamaska to Yamaska Sud-Est	0.99	21.5	2.0	1.8–2.3	1.7–8.3

Note: The distinction between the subindices IDEC-Neutral and IDEC-Alkaline was based on these natural pH values modeled from the geological characteristics of the sites (Grenier et al. 2006).

IDEC response time in relation to pH and trophic status

The response of the IDEC seemed to vary as a function of trophic status and translocation type (degradation or amelioration) (Table 4; Fig. 3). Regardless of the subindex used (IDEC-Neutral versus IDEC-Alkaline), the results suggested that the degradation of an assemblage was faster than its recovery. The response time of the IDEC as a function of the trophic status indicated that the time needed for a complete degradation or recovery increased with the trophic status. An additive linear model was used to test the relationships between response time (dependent variable; estimated from piecewise regressions) and trophic status ($\mu g \cdot L^{-1}$ total P, $\log_{10}$-transformed), pH (categorical variable: IDEC-Neutral or IDEC-Alkaline), and type of translocation (categorical variable: degradation or recovery). Because there are uncertainties about response time estimates, and therefore the reliability of these estimates varied broadly (Table 3), cases in the linear model were weighted proportionally to the inverse of the variance in response time yielded by the piecewise regressions. The linear model indicated that response time increased with trophic status ($P < 0.001$) and type of translocation ($P = 0.006$), with no apparent effect for pH ($P = 0.36$).

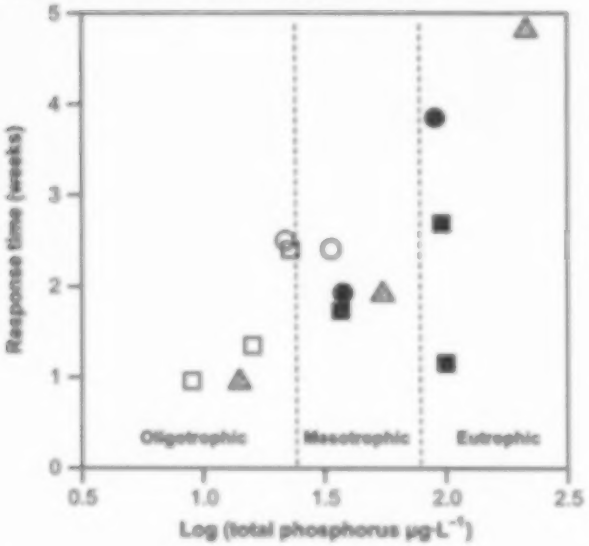
Discussion

The general objective of this study was to measure and model the response time of the IDEC following a translocation of diatom assemblages from an altered site to a reference site and vice-versa. The results indicate that the response to the simulated environmental conditions (mainly changes in nutrient concentrations) was more rapid for a degradation than for a recovery. The methods proposed here improve on previous work by providing quantitative estimates of turnover rate and their associated uncertainty in diatom assemblages. The frequency of sampling, duration (time after substrate translocation), and variety of site conditions in the present study provide strong evidence for an accelerated response of diatoms to a degradation (within a week in certain cases) and a slower path to recovery (up to 4 weeks for the Nicolet Sud-Ouest River). Based on the results from the piecewise regressions, a general model was proposed for the response of diatom assemblages as a function of environmental conditions, i.e., trophic status and type of simulated change (degradation or amelioration).

Variability in response time

de la Rey et al. (2008) showed that diatom species diversity tends to be higher at intermediate than at low levels of pollution. Lavoie et al. (2008*a*) also suggested that diatom assemblages are less diverse in oligotrophic environments than in mesotrophic and eutrophic environments and that there is a link between the trophic status of the ecosystem and the response time of diatom assemblages. Their study monitored the IDEC over time in three rivers and compared the IDEC values with phosphorus concentrations expressed as a one-time measurement and as averages over 1-week, 3-week, and longer periods. Their results and those of the present study indicate that the IDEC integrates variability over a period of time that is dependent on the trophic status of the river and the variability of nutrient concentrations. For example, in an oligotrophic river (Ste. Anne River), where nutrient concentrations were low and generally stable, an increase in phosphorus induced a rapid change in diatom assemblage structure and IDEC value within the following week. In a study conducted by Pan and Lowe (1994), algal assemblages dominated by *A. minutissimum*, *C. placentula*, and *Fragilaria ulna* were primarily phosphorus-limited and responded after only 6 days of nutrient enrichment. Their results were comparable with the 1-week interval between TP increase and IDEC value decrease found by Lavoie et al. (2008*a*) and the mean response time of 1.2 weeks in oligo-

Fig. 3. Relationship between response time of diatom assemblages and stream trophic status (μg·L^{-1} total phosphorus, $\log_{10}$-transformed). Different symbols and fill patterns are used to represent translocation types (recovery: open symbols; degradation: solid symbols) and pH status (alkaline: circles; neutral: squares). Data from Lavoie et al. (2008*a*) are also presented (gray triangles).



trophic rivers observed in the present study. In a mesotrophic river (Nicolet River), the response time observed by Lavoie et al. (2008*a*) was approximately 2 weeks. This result is also similar to the average 2.3 weeks observed in the present study for a response in the IDEC following a degradation or a recovery in mesotrophic environments. In a eutrophic river (Boyer River), Lavoie et al. (2008*a*) showed that diatom assemblages are adapted to frequent and major fluctuations in nutrient concentrations. In their study, the IDEC showed a slower response to short-term fluctuations and integrated nutrient concentrations over a period of 5 weeks. This period is longer than found in the present study, where the response time of the IDEC to a simulated amelioration of the water quality averaged 2.7 weeks in eutrophic conditions. Although interpretation of the effects of trophic status on response times in the present study must be tempered because trophic status was confounded with the type of translocation, the findings presented in Lavoie et al. (2008*a*) and in the present study suggest that oligotrophic rivers are more sensitive to nutrient variations than eutrophic rivers and that their diatom assemblages are markedly altered by nutrient increase. In contrast, diatom assemblages are less sensitive to nutrient fluctuations in eutrophic rivers, which are integrated more slowly into index values. A marked and prolonged change in TP concentration is required to provoke a change in diatom assemblage structure and IDEC values in eutrophic rivers. Lavoie et al. (2008*a*) proposed a relationship between river trophic status and temporal integration of TP concentrations by diatom assemblages. The response time of diatom assemblages modeled in the present study agrees with the temporal integration of TP concentrations proposed in their study.

Table 4. Average response time of the IDEC, Shannon's diversity index, and total phosphorous (TP) values following a simulated degradation or amelioration of the conditions.

	Average response time (weeks)	Shannon's diversity index	TP (μg·L^{-1})
Degradation	2.0	2.1	21
Recovery	2.4	2.7	72
Oligotrophic conditions*	1.2	2.0	13
Mesotrophic conditions*	2.3	2.6	31
Eutrophic conditions*	2.7	2.4	96

*Site classification based on trophic status followed the criteria in Dodds et al. (1998).

Iserentant and Blancke (1986) transferred artificial substrates between two streams characterized by different pollution levels in naturally circumneutral waters and observed that the assemblages responded more rapidly to the simulated degradation than to the simulated amelioration. In their study, the sudden water quality degradation was accompanied by a marked reduction of pollution-sensitive taxa and a large increase in pollution-tolerant taxa within 4 weeks after the translocation. They noted drastic changes in assemblage structure 2 weeks after the translocation to the impacted site, whereas 45 days were not sufficient for a complete turnover of the assemblage in the case of recovery. Ivorra et al. (1999), Tolcach and Gómez (2002), and Gold et al. (2002) also found that diatom assemblages in naturally circumneutral environments achieved greater turnover when translocated to a polluted site (within 2 weeks) than when translocated to a reference site. Hirst et al. (2004) also observed that the response of diatom assemblages to a sudden acidification of the environment was faster than the return to normal conditions. The sensitivity of different European diatom indices was studied by Rimet et al. (2005) in a translocation experiment simulating an amelioration of the conditions in an environment with naturally alkaline water pH. Their results indicated that most of the changes in the assemblages were observed during the first phase of the sampling strategy, 20 to 30 days after the transfer.

Complexity of the diatom assemblages

It is possible that the nutrients accumulated in the biofilm might have sustained the diatoms for a period of time. This process has been observed in water courses and lakes undergoing restoration, where nutrients included in the sediments and in the biota continued to be available for a period of time and therefore slowed down the recovery process. However, in this study, the colonization of the substrate took place over a period of 4 weeks, allowing for the establishment of a mature diatom community. Although the communities were mature and similar to what was observed on natural substrates, there was no thick accumulation of biomass on the substrates, which might have limited the diffusion of nutrients after substrate translocation.

The variation in response time as a function of trophic status may in part be related to the diversity and complexity of the assemblages prior to translocation. The results from this study suggest that the assemblages sampled in the selected oligotrophic sites respond more rapidly to an alteration (reflecting mainly an increase in nutrients). This

difference in response time may be due to a sudden decrease in abundance of dominant taxa that are sensitive to eutrophication. It seems unlikely that the longer response time observed in the mesotrophic and eutrophic environments could be attributed to differences in colonization rates. Most of the dominant taxa at all sites were present at varying abundances during the whole sampling period. Colonization likely played only a minor role in modifying abundances. Instead, the longer integration period in mesotrophic and eutrophic environments may be attributed in part to the complexity of the diatom assemblage and the tolerance of the taxa. This result suggests that the complexity of the assemblages influences the time needed for assemblage restructuring. In an assemblage dominated by numerous pollution-tolerant taxa, there are no drastic changes in assemblage structure following a change in environmental conditions because responses can be highly variable among taxa. However, in an assemblage dominated by only a few taxa, a change in the abundance of a taxon will rapidly influence the structure. Diversity–stability relationships have been the subject of numerous theoretical and empirical studies in ecology (e.g., MacArthur 1955; May 1973; Steiner et al. 2006). Our results agree with previous studies on assemblage resistance and resilience, which found that population and assemblage diversity influence the temporal stability (e.g., McCann 2000; Cottingham et al. 2001). The results suggest that more diverse diatom assemblages are more stable and more resistant to nutrient variations in the environment. The response time seems, therefore, attributed to the sensitivity (resistance) of the taxa to fluctuations in nutrients and to the complexity of the assemblage (resilience). The results obtained in the present study also reflect the hysteresis process described in Beisner et al. (2003) in lake eutrophication, where the responses to reduction and increase in nutrient inputs do not simply follow the same trajectories in opposite directions. As stated by Lake et al. (2007), for a variety of causes, such as different dispersal capabilities, priority effects, and the playing out of interactions, it may take a longer time to fully restore an assemblage to the targeted state than to degrade it. Thus, the restoration pathway may show hysteresis or follow Sarr's (2002) "broken leg" model, in which the assemblage follows a lengthy and nonlinear trajectory to recovery. In the case of diatoms, more diverse assemblages often result when environmental conditions are perturbed (e.g., eutrophication). The taxa may have different sensitivity to pollution, but will generally be less sensitive to the frequent fluctuations in nutrient concentrations characterizing mesotrophic and eutrophic environments. These assemblages are more resilient and complex. The return to the original assemblage will necessitate a longer time because the tolerant taxa are capable of supporting a decrease in nutrient concentrations for a certain period of time before the pollution-sensitive taxa recolonize and become dominant again.

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Appendix A

Appendix A continues on the following page.

Table A1. Changes in the relative proportions of the dominant species after 12 weeks in the hosting sites for (*a*) subindex IDEC-Neutral and (*b*) subindex IDEC-Alkaline.

(*a*) IDEC-Neutral

Degradation

Noire to Blanche		Shawinigan upstream to downstream		Ste. Anne to Des Envies	
% of dominant species at week 0	% of dominant species at week 12	% of dominant species at week 0	% of dominant species at week 12	% of dominant species at week 0	% of dominant species at week 12
TFLO = 41.0	ASHU = 16.1	ADMI = 30.4	GOMP1 = 26.0	ADMI = 38.6	ARIV = 14.5
EUNO = 17.7	NGER = 8.8	ADMCF1 = 15.3	ESLE = 13.5	TFLO = 20.2	PTLA = 9.4
EBIL = 5.5	MVAR = 8.3	EUNO = 5.7	NGRE = 9.2	BBRE = 10.1	CPLE = 8.0
EINC = 3.6	ESLE = 6.4	SPIN = 5.4	ADMI = 8.7	EUNO = 5.5	ADMI = 7.5
BBRE = 2.9	NPAD = 5.7	TFLO = 4.5	NPAD = 7.0	FCAPF = 2.9	NAMP = 6.3

Recovery

Blanche to Noire		Shawinigan downstream to upstream		Des Envies to Ste. Anne	
% of dominant species at week 0	% of dominant species at week 12	% of dominant species at week 0	% of dominant species at week 12	% of dominant species at week 0	% of dominant species at week 12
RSIN = 26.6	EUNO = 20.8	CPLE = 35.2	ADMI = 16.0	NPAD = 9.9	ADMI = 22.7
CPLE = 10.9	BBRE = 12.6	RSIN = 28.1	CPLE = 13.6	NPAL = 7.2	TFLO = 14.4
ARIV = 10.1	TFLO = 10.7	ADMI = 10.2	ARIV = 9.7	NGRE = 5.0	BBRE = 4.9
ESLE = 8.5	EBIL = 6.8	ARIV = 5.5	EUNO = 6.1	ARIV = 4.8	FCAPF5 = 4.1
PTLA = 8.0	CPLE = 5.6	ESLE = 5.0	TFLO = 3.9	NCRY = 4.8	BMIC = 3.2

(*b*) IDEC-Alkaline

Degradation

Nicolet to Nicolet Sud-Ouest		Yamaska Sud-Est to Yamaska	
% of dominant species at week 0	% of dominant species at week 12	% of dominant species at week 0	% of dominant species at week 12
ADMI = 41.7	NCPR = 15.3	ARIV = 52.2	NCPR = 14.9
RSIN = 15.9	CPLE = 11.4	ADMI = 11.9	ADMI = 12.5
CPLE = 9.8	MVAR = 11.2	ADLA = 9.2	CPLE = 10.6
NPAD = 3.2	NPAD = 9.7	ESLE = 3.7	NGRE = 6.7
ESLE = 2.9	NTPT = 5.4	FCAPF5 = 3.7	ESLE = 6.3

Recovery

Nicolet Sud-Ouest to Nicolet		Yamaska to Yamaska Sud-Est	
% of dominant species at week 0	% of dominant species at week 12	% of dominant species at week 0	% of dominant species at week 12
CPLE = 29.9	ADMI = 32.7	MVAR = 13.3	ADLA = 22.3
RSIN = 20.4	NCPR = 7.3	ESLE = 9.5	ADMI = 17.2
ADMI = 10.6	NPAD = 7.3	NCPR = 9.3	ARIV = 16.7
NCTE = 3.5	NTPT = 6.5	ADMI = 8.1	GENT = 7.4
NINC = 3.3	CPLE = 6.3	FCAPF5 = 4.7	AMSA = 3.4

Note: ADLA = *Achnanthidium* cf. *latecephalum* Kobayasi 1997; ADMCF1 = *Achnanthidium microcephalum* (Kützing) 1844 form 1; ADMI = *Achnanthidium minutissimum* (Kützing) Czarnecki 1994; AMSA = *Achnanthes minutissima* var. *saprophila* Kobayasi & Mayama 1982; ARIV = *Achnanthidium rivulare* Potapova & Ponader 2004; ASHU = *Achnanthes subhudsonis* Hustedt 1921; BBRE = *Brachysira brebissonii* Ross 1986; BMIC = *Brachysira microcephala* (Grunow) Compère 1986; CPLE = *Cocconeis placentula* var. *euglypta* (Ehrenberg) Grunow 1884; EBIL = *Eunotia bilunaris* (Ehrenberg) Mills 1934; EINC = *Eunotia incisa* Gregory 1854; ESLE = *Encyonema silesiacum* (Bleisch) Mann 1990; EUNO = *Eunotia* spp.; FCAPF5 = *Fragilaria capucina* Desmazières 1825 form 5; GENT = *Gomphonema entolejum* Østrup 1903; GPAR = *Gomphonema parvulum* (Kützing) Kützing 1849; MVAR = *Melosira varians* Agardh 1827; NAMP = *Nitzschia amphibia* Grunow 1862; NCPR = *Navicula capitatoradiata* Germain 1981; NCRY = *Navicula cryptocephala* Kützing 1844; NCTE = *Navicula cryptotenella* Lange-Bertalot 1985; NGER = *Navicula germainii* Wallace 1960; NGRE = *Navicula gregaria* Donkin 1861; NINC = *Nitzschia inconspicua* Grunow 1862; NPAD = *Nitzschia palea* var. *debilis* (Kützing) Grunow 1880; NPAL = *Nitzschia palea* (Kützing) W. Smith 1856; NTPT = *Navicula tripunctata* (Müller) Bory 1822; PTLA = *Planothidium lanceolatum* (Brébisson) Round & Bukhtiyarova 1996; RSIN = *Reimeria sinuata* (Gregory) Kociolek & Stoermer 1987; SPIN = *Staurosirella pinnata* (Ehrenberg) Williams & Round 1987; TFLO = *Tabellaria flocculosa* (Roth) Kützing 1844.

Historical abundance of Puget Sound steelhead, *Oncorhynchus mykiss*, estimated from catch record data

N. Gayeski, B. McMillan, and P. Trotter

Abstract: We used reported commercial catch data and historical information regarding unreported catches to estimate the abundance of winter steelhead, *Oncorhynchus mykiss*, in Puget Sound rivers in 1895, the year in which the peak commercial catch of steelhead occurred. We employed a Bayesian analysis to address the uncertainties associated with the estimation process and report abundance estimates for four large northern Puget Sound rivers and for the remaining aggregate of rivers and streams in Puget Sound. The central 90% of the posterior distribution of total abundance ranged from 485 000 to 930 000, with a mode of 622 000. Compared with the 25-year average abundance for all of Puget Sound of 22 000 for the 1980–2004 period, our results show that current abundance is likely only 1%–4% of what it was prior to the turn of the 20th century. Loss of freshwater habitat alone can account for this reduction in abundance only if there was an extraordinary decline in productivity. Our estimates of historical abundance should better inform the development of recovery goals for Puget Sound steelhead.

Résumé : Nous utilisons les données des déclarations des pêches commerciales, ainsi que des informations historiques au sujet des récoltes non déclarées, pour estimer l'abondance de la truite arc-en-ciel anadrome, *Oncorhynchus mykiss*, d'hiver dans les rivières de Puget Sound en 1895, l'année durant laquelle s'est produite la pêche commerciale de truites arc-en-ciel anadromes la plus importante. Une analyse bayésienne nous a servi à tenir compte des incertitudes reliées au processus d'estimation et à évaluer l'abondance dans quatre grandes rivières du nord de Puget Sound et pour l'ensemble des autres rivières et ruisseaux de Puget Sound. Les 90 pour cent du centre de la distribution a posteriori de l'abondance totale varient de 485 000 à 930 000, avec un mode à 622 000. Étant donné la moyenne sur 25 ans de l'abondance de 22 000 pour l'ensemble de Puget Sound pour la période 1980–2004, nos résultats montrent que l'abondance actuelle est vraisemblablement seulement de 1%–4% de ce qu'elle était à la fin du dix-neuvième siècle. La perte des habitats d'eau douce par elle-même peut expliquer cette réduction de l'abondance seulement s'il y a eu un déclin extraordinaire de la productivité. Nos estimations de l'abondance dans le passé devraient fournir une base plus solide pour la mise au point de cibles de récupération pour les truites arc-en-ciel anadromes de Puget Sound.

[Traduit par la Rédaction]

Introduction

Steelhead, *Oncorhynchus mykiss*, in the Puget Sound evolutionarily significant unit (ESU) were recently listed as threatened under the US Endangered Species Act (ESA) (Hard et al. 2007; Rausch 2007), prompting the initiation of recovery planning. Recovery planning requires, ultimately, the identification of conditions under which the ESU can be considered to have been recovered and delisted. Prominent among the factors ESA recovery planning must typically address is the rebuilding of population numbers and related life history characteristics such as age and size structure. To this extent, recovery under ESA confronts many of the same problems and controversies that have arisen in discussions of the rebuilding of overfished marine stocks. We agree with Rosenberg et al. (2005, p. 84) that "[i]n the current policy debate about rebuilding depleted fisheries and restoring marine ecosystems, it is important to recognize that fisheries for key commercial species like cod were far more productive in the past. As we attempt to rebuild these fisheries, our decisions should reflect real and realistic goals for management, not just recently observed catch levels."

We believe that the same caution applies to Pacific salmon (*Oncorhynchus* spp.) and steelhead recently listed under the ESA. Whenever possible, recovery planning should endeavor to compare current levels of abundance not only with the levels that immediately preceded ESA listing, but with historical estimates of productivity and abundance as well. Without such an historical perspective, it is impossible to know whether or not recovery targets may underestimate the potential abundance and diversity that is required to assure the persistence of delisted populations.

However, the absence of high-quality quantitative data regarding population abundance and dynamics, of the sort rec-

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ognized today as necessary for proper fish population management, poses a considerable challenge for translating historical information into appropriate quantitative terms. In this paper, we show how several kinds of available historical information for Puget Sound steelhead can be used to estimate historical abundance. We use a Bayesian analysis framework to estimate steelhead run sizes from early records of commercial catch data for the Puget Sound region and other local history sources.

The objectives of this paper are threefold. Our first objective is to provide an evidence-based estimate of steelhead run size in Puget Sound shortly before the turn of the 20th century. While not completely representative of pristine conditions of productivity and abundance of Puget Sound steelhead, estimated abundance at this point in time was considerably greater than the levels that were obtained in the three decades preceding the listing of Puget Sound steelhead in 2007, and together with information on habitat losses, this provides an important perspective on the productive potential of the Puget Sound ESU under current conditions.

Our second objective is to illustrate how quantitative and narrative historical fisheries and socio-economic information can be integrated and employed to obtain credible quantitative estimates of population sizes and conditions that properly acknowledge the uncertainties that are inevitable in such an endeavor. Our third objective is to scale our historical estimates to current and historic estimates of habitat quantity so that our estimates may provide an informative perspective on the productive potential of Puget Sound steelhead under current conditions.

We address the first and second objectives by employing turn-of-the-20th-century (1895) reported commercial catch data for Puget Sound steelhead, along with historical information pertaining to the development of activities resulting in unreported catch of steelhead, to estimate the terminal run sizes of steelhead in Puget Sound. To accomplish our third objective, we employ recent estimates of the amount of habitat in Puget Sound rivers and streams currently available to steelhead as well as estimates of the proportion of steelhead habitat lost since the turn of the 20th century to compare our estimates with current conditions. We then compare both our historic abundance estimates and our habitat-corrected estimates with recent estimates of Puget Sound steelhead run sizes.

To be consistent with the way these early records were compiled, we define the Puget Sound region to include not only the streams draining into Puget Sound itself up to and including the Nooksack River near the Canadian border, but also the streams discharging into Hood Canal and the Washington side of the Strait of Juan de Fuca westward to (but not including) the Makah Indian Reservation. Some streams in this region host two races of steelhead, commonly referred to as winter-run and summer-run, owing to the timing of their entry into their natal streams and their state of sexual maturity when they do so. We limited our analysis to the winter run because, again, the earliest available written records are from fisheries that operated in winter specifically to harvest these steelhead (Collins 1892; Wilcox 1898; Rathbun 1900).

Materials and methods

Sources of historical data

Our source of historical winter steelhead harvest information was a series of reports on commercial harvest in west coast fisheries published by the old US Commission of Fish and Fisheries (Collins 1892; Wilcox 1895, 1898, 1902, 1906; Rathbun 1900; Cobb 1911, 1917, 1921, 1931). The first commercial harvest records for steelhead in Washington date from 1889, the year of statehood (Collins 1892). Commercial fishing in Puget Sound streams is known to have begun much earlier, with American settlers on the Puyallup and Duwamish rivers in 1853 (Anonymous 1853; Morgan 1951), and even prior to that, salmon and steelhead occasionally were accepted in trade at the Hudson Bay Company's Fort Nisqually for consumption at the post (Journal of Occurrences at Nisqually House 1833; Carpenter 1986). But while commercial fishing grew and shifted to other streams in the years following, catch records for this activity went unreported until 1889 (Collins 1892). The reported commercial harvest of steelhead in the Puget Sound region showed a growing trend over the first three periods of actual record, with the peak of reported commercial harvest occurring in 1895 (Wilcox 1898), after which steelhead catches declined (Rathbun 1900; Wilcox 1902, 1906; Cobb 1911, 1917, 1921, 1931), even though commercial effort to catch them did not, so we selected that data set for our analysis. The 1895 data likely reflect the abundance of Puget Sound steelhead populations in the late 19th century immediately preceding the buildup of a directed commercial fishery and, therefore, provides the best quantitative data from which to estimate the abundance of these populations. This follows the lead of the Biological Review Team of NOAA Fisheries, who likewise restricted its own examination of the historical record to the same 1895 data set when it updated its status review of Puget Sound steelhead for the Endangered Species Act (Biological Review Team 2005).

In addition to listing the total commercial catch of steelhead for the Puget Sound region as a whole, the Wilcox (1898) report also listed river-by-river commercial catches for four individual Puget Sound streams in 1895: the Nooksack, Skagit, Stillaguamish, and Snohomish rivers. We augmented this data set with information about the pace and extent of settlement and development from local history sources, including Immigration Society of North-Western Washington (1880), Local Committee of Pioneers (1906), Smith and Anderson (1921), Jeffcott (1949), Edson (1968), Bacon (1970), Clark (1970), Strickland (1984), and White (1992).

Although this data set gave us a solid basis for determining the commercial harvest level for steelhead at its historical peak, it did not include tribal subsistence catches (White 1992), nor did it include catches by "ranchers" for home uses, which, according to Wilcox (1898), were substantial in the aggregate and probably the equal of the commercial harvest. We could find no information regarding sport fishing for steelhead during this period. We accounted for the uncertainty associated with all of this off-the-books harvest as well as certain other uncertainties associated with this historical data set through the use of Bayesian estimation methods as described below. All catch data in Wilcox

(1898) were reported in pounds of fish, not numbers of fish. We inserted the data as reported (in pounds; 1 pound = 0.453 kg) and allowed our algorithms to make the appropriate conversions to numbers of fish.

Bayesian estimation of historical run sizes

For the four individual Puget Sound rivers singled out in the Wilcox (1898) report, and for the remaining rivers and streams in the Puget Sound region overall, we used a Bayesian analysis framework to estimate steelhead run sizes from the reported commercial catch data. The Bayesian approach typically treats the data as fixed (known) and the parameter of interest (in our case, the total steelhead run size, N) as unknown and conducts an inference on N by assuming a process involving N by which the data are generated. The hypothesized process is expressed in an equation known as the likelihood. Distributions (typically called "prior distributions" or "priors" for short) are specified for the unknown parameters of the likelihood, including N itself. The inference from the data via the likelihood produces a (posterior) probability distribution for N. In our case, in addition to the reported commercial catch data, our estimates depend on three unknown parameters: (*i*) the total steelhead catch that was unreported or otherwise not included in the reported commercial catch; (*ii*) the average mass of the steelhead caught; and (*iii*) the harvest rate on the total run that produced the total catch. Although we could not identify definitive point estimates for any of these three parameters, we were able to identify reasonable limits within which their true values are most likely to lie. Thus, we could delimit the extent of the uncertainties of the estimates of these parameters and employ them in our Bayesian analysis framework.

We chose the binomial likelihood on which to base our inference, where T (total catch) $\sim$ Bin(N, R), R being the harvest rate. Thus, we view the catch data as resulting from a binomial sampling of the total run N, at an average harvest rate R, as expressed by this likelihood equation:

$$(1) \qquad P(T|N,R) = \binom{N}{T} \cdot T^{R} \cdot (N-T)^{(1-R)}$$

where N is total run size, T is total catch in numbers of fish, and R is harvest rate.

The Bayesian inference proceeds by specifying appropriate (prior) distributions for R and N. To employ this approach, however, we first had to expand the reported commercial catch, C, to arrive at an estimate of T. This was done as follows. The reported commercial catch C was multiplied by a quantity U that represents the ratio of unreported catch to reported commercial catch to arrive at a figure for the unreported catch (in pounds). This number was then added to the reported catch to derive a number for the total catch (in pounds). Next, the total catch was divided by the average mass (in pounds) of the steelhead caught, M, to attain a figure for T. Thus:

$$(2) \qquad T = (C + C \cdot U), \text{ or equivalently, } T = C \cdot (1 + U)/M$$

where T is total numbers caught, C is the reported commercial catch, U is the ratio of unreported catch to reported commercial catch, and M is the average weight of steelhead caught (in pounds).

However, the only firm figure in eq. 2 is C. Uncertainty surrounds the values of U and M. These uncertainties required that we place distributions on both U and M and repeatedly apply the algorithm to arrive at a value for T (eq. 2) by drawing different values of U and M from the respective distributions. Consequently, we were required to generate a distribution of values of T for each value of C reported for each of the five populations (four rivers and the remaining aggregate of Puget Sound rivers and streams). Thus, our Bayesian analysis is somewhat atypical in that our inference on N is conducted on values of T that are themselves uncertain and consequently are represented by a distribution (the distribution of T). Note also that since the estimation process evaluates the likelihood of each value of N drawn from the prior on N for a large random sample of values drawn from the prior on R and the distribution of T, the posterior distribution of N will be distributed as a beta binomial rather than as a simple binomial, and thus the variance will be much broader than expected under a simple binomial.

All calculations and the inference on N were programmed and carried out using the Fortran shell program SWL (sampling weighted likelihood; written by Daniel Goodman, Environmental Statistics Group, Department of Biology, Montana State University, Bozeman, Montana). SWL samples the prior distributions by direct simulation with calls to random number generators and then weights each sampled set of values of parameters by their likelihood, cumulating histograms and posterior summaries of the sampled parameter values weighted accordingly. This contrasts with sampling or resampling the joint posterior as Markov chain Monte Carlo approaches do. This is extremely efficient for calculations of low dimension (four or fewer parameters) as is the case here with four unknown parameters: N, R, U, and M. This efficiency enabled us to employ ten million samples of all prior distributions and to calculate the posterior distributions of all quantities of interest from these samples using little computer time. We chose uniform distributions for the unknown parameters N, R, U, and M, with upper and lower limits selected on biological and historical grounds to bracket the most likely range within which the true parameter values lie (listed in Table 1).

For each of the five populations, random values of N, R, U, and M were drawn from the respective prior distributions, and eq. 2 applied to the values of U, M, and the population-specific value of C (in pounds) to generate a sample value of T. A posterior value of N was then obtained by calculating the likelihood of N (eq. 1) from the values of N, R, and the derived sample value of T (details of the calculation are described in further detail in Appendix A). By sampling 10 000 000 random combinations of N, R, U, and M, we were assured of adequately sampling the joint parameter space. To improve efficiency, we included a trap that redrew random values of U and M when any derived value of T was larger than the value of N drawn from the prior on N.

For reporting and histogram display of the posterior probabilities, the intervals spanned by the prior probabilities were divided into 100 equal-sized bins. This enabled us to display histogram outputs as smooth continuous curves and to evaluate the probabilities of narrow ranges of parameter values. We examined posterior histograms and related sum-

Table 1. Reported commercial catch for 1895, estimated currently (SC) and maximum historically (SH) accessible stream lengths (km), and prior distributions.

Population	*C*	SC (SH)	*M*-LO	*M*-HI	*U*-LO	*U*-HI	*R*-LO	*R*-HI	*N*-LO	*N*-HI
Nooksack	660 160	612 (918)	7.0	9.5	0.10	0.30	0.60	0.90	80 000	225 000
Skagit	205 190	982 (1473)	7.0	9.5	0.50	1.0	0.30	0.60	50 000	200 000
Stillaguamish	180 000	445 (667.5)	7.0	9.5	0.50	1.0	0.40	0.70	40 000	130 000
Snohomish	401 620	926 (1389)	7.0	9.5	0.50	1.0	0.40	0.70	90 000	290 000
Remainder	518 582	4014 (6021)	7.0	9.5	0.50	1.0	0.40	0.70	100 000	370 000

Note: *C*, reported commercial catch (pounds; 1 pound = 0.453 kg); *M*-LO and *M*-HI, average low and high masses of steelhead caught (pounds); *U*-LO and *U*-HI, low and high ratios of unreported catch to reported commercial catch; *R*-LO and *R*-HI, low and high harvest rates; *N*-LO and *N*-HI, low and high numbers of fish (i.e., run size).

maries of marginal parameter probabilities for total run size, *N*, numerical catch, *T*, and harvest rate, *R*.

Justification of the prior distributions

The limits placed on the priors of all unknown parameters are listed, as well as the specific values of the total reported 1895 commercial catch (in pounds) and the estimated value of currently accessible stream length for each of the four reported rivers and for the remainder of Puget Sound rivers and streams (Table 1).

The distribution of average steelhead mass, M

Steelhead returning to Puget Sound rivers and streams can range from 1.5 pounds to well over 15 or 16 pounds; however, data on numbers and total mass of commercially caught steelhead reported by the Washington State fish commissioner in 1892 yielded an average mass of 8 pounds per steelhead (Crawford 1892). Also, data developed in the 1940s and 1950s for returns to several individual rivers yielded average masses ranging from 7.0 to 9.4 pounds (e.g., Meigs and Pautzke 1941; Larson and Ward 1955; Withler 1966). Therefore, we reasoned that the true average mass of steelhead for the aggregate of Puget Sound rivers and streams should fall within limits of 7.0 and 9.5 pounds.

There is evidence that fishing with gill nets, as was practiced by Native American subsistence fishermen and later by Puget Sound's commercial fishermen, may selectively capture the larger fish in an annual run, thereby exerting a selective pressure for smaller average size in subsequent returns (Hard et al. 2008). Although it could be argued that tribal and commercial fishing could have produced such a result by the time the studies we relied on for our limits on the prior for *M* were undertaken, observations in the zoological report of the Pacific railroad survey of 1853–1855, compiled before commercial fishing got under way to any major extent, indicate that this was not the case for Puget Sound steelhead (Suckley 1860); average sizes and masses appeared to be about the same then as prevailed during the 1940s and 1950s.

The prior on harvest rate R *and the distribution of unreported/reported catch* U

The 1895 commercial catch was the largest catch of Puget Sound winter-run steelhead in the record for the period 1889–1915, culminating the period of rapid buildup of the commercial fishery following statehood in 1889 (e.g., Collins 1892; Wilcox 1898; Cobb 1917). Of the four northern Puget Sound rivers of our primary examination, the commercial fishery on the Nooksack was the most intense and well-developed due in large part to the earlier and sustained industrial development of Bellingham, Washington, which was the commercial heart of the young state north of Seattle until Everett became a sustainable industrial site after 1895 (e.g., Bacon 1970; Clark 1970; Edson 1968). For the same reasons that led to the commercial–industrial development of Bellingham, agricultural settlement of the Nooksack basin by Euro-Americans lagged well behind that on the Skagit, Stillaguamish, Snohomish, and other smaller rivers basins in central and south Puget Sound (cf. Jeffcott 1949). Relative to the size of the Nooksack basin, the commercial catch alone was particularly large, greatly exceeding not only the catch on the other three large rivers but the catch from all remaining rivers in Puget Sound combined (Table 1).

Given the intensity of the commercial fishery and the relative magnitude of the 1895 catch, we determined that the unreported Nooksack catch most likely accounted for a relatively small proportion of the total catch compared with the other rivers. Historic accounts indicate unreported catch was particularly related to agricultural use of anadromous fish runs as fertilizer and livestock feed as well as rural subsistence (Local Committee of Pioneers 1906; Jeffcott 1949; White 1992). We estimated that it was, nonetheless, at least 10% of the reported Nooksack commercial catch but unlikely to have been any greater than 30%, and so bounded *U* by 0.1 and 0.3.

Taking into account both reported and unreported catches, we estimated that the total harvest rate on the Nooksack run was likely to have been particularly high. Specifically, we estimated that the total harvest rate could not have been lower than 60% but was unlikely to have been higher than 90%. So we bounded the prior for the Nooksack between these values.

The commercial fishery on the Skagit was the last to develop among the large river basins in Puget Sound, with fishermen just beginning to learn the run timings during the first 1895 reported catch period (Wilcox 1898). The nonreported catch related to agricultural use, in particular, was of great magnitude (Local Committee of Pioneers 1906; White 1992), probably equaling the commercial catch as reported for steelhead in 1895 on the Stillaguamish River (Wilcox 1898). We therefore chose to bound *U* for the Skagit and for all other rivers by 0.5 and 1.0. In other words, we assume that the unreported catch in these rivers was at least half of the reported commercial catch, and Wilcox (1898) states "probably" equaled it. Despite the relatively undeveloped state of the commercial fishery on Skagit steelhead, the reported catch was still considerable (Table 1), but in view

of the size of the basin, we estimated that the total harvest rate was likely lower than on the Nooksack, perhaps as low as 30%, but no greater than 60%.

The Stillaguamish and Snohomish river basins were both closer to developing commercial centers in Everett and Seattle (Wilcox 1898; Clark 1970) than the Skagit but also had considerable agricultural development with related unreported catch probably high (e.g., Wilcox 1898; Local Committee of Pioneers 1906; White 1992). The reported commercial harvest from both rivers was nearly proportional to estimated accessible stream lengths in each basin (SH, Table 1) and greater than that in the Skagit but much less than that in the Nooksack. We therefore estimated that the total harvest rate was unlikely to be lower than 40% but no greater than 70%.

Most of the rivers and streams comprising the remaining Puget Sound steelhead populations were individually smaller than the Skagit or Snohomish and were likely of variable productivity. Most had likely experienced early levels of settlement and agricultural development comparable to the Skagit, Stillaguamish, and Snohomish (e.g., Local Committee of Pioneers 1906; Edson 1968; Steilacoom Historical Museum Association 2009), so we assumed that the total of the unreported catch bore a similar proportion to the reported catch as in the larger rivers. Thus, we bounded U between 0.5 and 1.0 as for the others. We also assumed that the total harvest pressure was comparable to that estimated for the Stillaguamish and Snohomish, and so bounded R between 0.4 and 0.7. This assumption is particularly conservative given that the reported commercial catch is substantially smaller relative to total accessible stream length (Table 1). Lower harvest rates would result in larger posterior estimates of total run size than those we arrived at. As previously noted, we found no information concerning the magnitude of sport fishing for steelhead during this period. The fact that it escaped mention in the numerous historical sources we did consult suggests that sport fishing during this period constituted a small fraction of the off-the-books steelhead catch. If major sport fishing catch did occur in any of the Puget Sound rivers, our failure to include it in the analyses would only have the effect of further underestimating U and thus the total catch T. The magnitude of the resulting underestimation of T is unlikely to be considerable enough to affect the range of the priors on R, and thus we believe the net effect would be to underestimate the run sizes.

Distributions for run size, N

No information was available that would have permitted us to estimate an informative unimodal or multimodal prior distribution for N for any of the four rivers or the remainder of Puget Sound. We therefore chose uniform distributions with lower limits slightly less than the lowest values of T, knowing that the estimation algorithm would exclude values less than T as explained above. Upper limits on N were chosen by trial and error to provide limits slightly larger than the largest value of N in the posterior distribution. In this way we allowed the likelihood to entirely dominate the calculation of the posterior distribution, in keeping with the intention that the priors for N be uninformative. This approach will have the effect of inflating the posterior variance of N compared with a case in which an independent prior is chosen such that a portion of the posterior probability mass is constrained to "pile up" at the upper or lower boundaries of the prior.

Comparison of historical with contemporary run size

To compare our estimates of 1895 run sizes with current conditions, we used NOAA Fisheries' estimates of recent average abundances presented in the 2005 Status Review of Puget Sound Steelhead (Biological Review Team 2005, their table 5). This table presents run size estimates averaged for all years between 1980 and 2004 for which data were available, and for the most recent 5 years prior to the date of the review (2000–2004), for all rivers except the Nooksack. The only recent run size data available for the Nooksack is from the 2003–2004 return year when 1598 wild steelhead returned (WDFW 2006). We rounded this to 1600 and used this number for both the 25- and 5-year averages for the Nooksack. These contemporary run sizes are presented for the five populations for which we provided estimates of 1895 run size (Table 2).

To further facilitate comparison and interpretation of these numbers, we translated them into fish-per-accessible-stream-kilometre (FKM) using recent NOAA Fisheries estimates of stream lengths within river basins that are currently accessible to returning adult steelhead (D. Holzer, NOAA–NMFS Northwest Fisheries Science Center, 2725 Montlake Boulevard East, Seattle, WA 98112, USA, personal communication, 2009; cf. also Beechie et al. 2001). Based on additional discussions with NOAA staff (D. Holzer and T. Beechie, personal communications, 2009, 2010), we estimated that the maximum proportion of habitat accessible to steelhead in any river basin in 1895 that has been lost during the 20th century is 33% (that is, we estimate that currently accessible stream lengths are two-thirds the total lengths available in 1895). Washington Department of Fish and Wildlife recently estimated the percentage of winter steelhead stream habitat lost in Puget Sound during the 20th century to be 21% (Scott and Gill 2008). We chose the larger NOAA estimate as being more conservative and used this larger habitat loss figure to estimate the maximum length of stream kilometres (SH) accessible to steelhead in 1895. Thus, we multiplied current accessible stream lengths (SC in Table 1) by 1.5 to generate estimates of SH for each of the five populations (SH in Table 1). We then divided the posterior mode and posterior 5th-percentile estimates of N by the SH value for each population to produce modal and 5th-percentile posterior estimates of FKM (Table 3). We also divided the two mean run size estimates of the same populations under current conditions by the SC value for each to produce estimates of FKM for the 1980–2004 and 2000–2004 averages (Table 2).

Results

Estimates of historical catch (T), harvest rates (R), and run sizes (N)

The posterior distribution of the parameter N, the distribution of T, and the posterior distribution of the parameter R for the Snohomish River basin are displayed (Figs. 1–3).

These distributions are representative of the shapes of the

Table 2. Puget Sound (PS) steelhead run sizes from NOAA Fisheries 2005 Status Review.

	N			FKM	
Population	1980–2004	2000–2004	SC	All years	5 years
Nooksack*	1600	1600	612	2.6	2.6
Skagit	6993.9	5418.8	982	7.12	5.52
Snohomish	5283	3230.1	926	5.71	3.49
Stillaguamish	1027.7	550.2	445	2.31	1.24
Rest of PS	6673.8	4742.5	4014	1.69	1.18
All of PS	21678	15542	6979	3.1	2.2

Note: *N*, average wild run sizes for 1980–2004 and for 2000–2004; SC, current estimates of accessible stream lengths; FKM, equivalent fish-per-accessible-stream-kilometre.
*Data for 2003–2004 from page 18 of the appendix "Puget_stid_esu" in Scott and Gill (2008).

Table 3. Estimated 1895 Puget Sound (PS) steelhead abundance (*N*), estimates of historically accessible stream lengths (SH), and equivalent fish-per-accessible-stream-kilometre (FKM).

Population	Posterior mode *N*	Posterior 5th percentile *N*	SH	FKM, mode *N*	FKM, 5th percentile *N*
Nooksack	127800	101400	918	139	110
Skagit	86700	70000	1473	59	48
Snohomish	153000	114000	1389	110	82
Stillaguamish	69200	51700	667.5	104	77
Rest of PS	185000	148000	6021	31	25
All of PS	621700	485100	10469	59.4	46.3

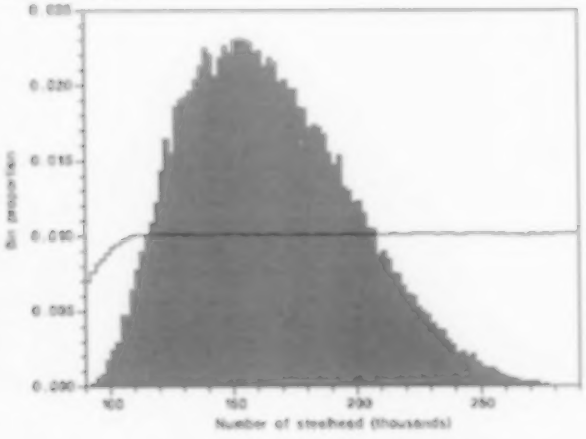


Fig. 1. Posterior distribution of total steelhead run, *N*, for the Snohomish River in 1895: (mean = 164 500; mode = 153 000; standard deviation = 33 400; central 90% of the posterior distribution: 114 000–224 000).

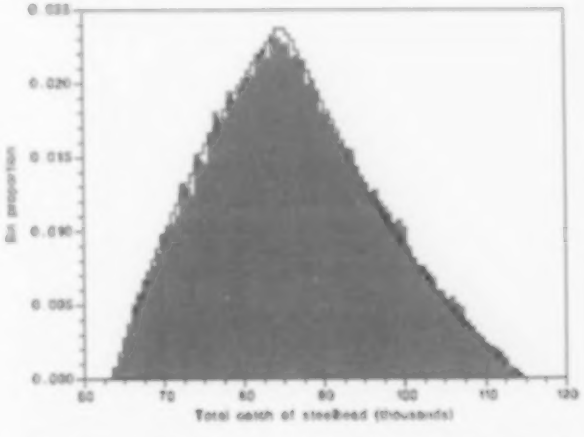
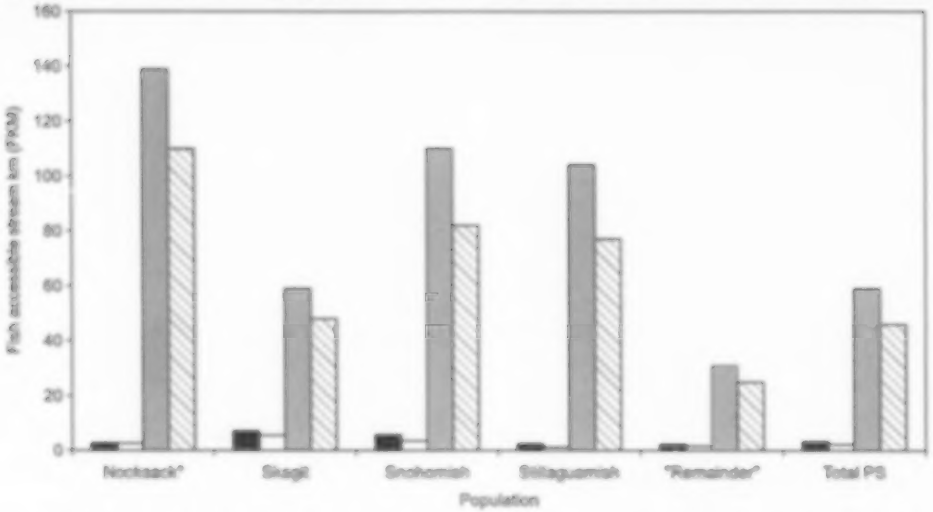


Fig. 2. Distribution of the total numerical catch of steelhead, *T*, for the Snohomish River in 1895: (mean = 85 900; mode = 83 700; standard deviation = 10 400; central 90% of the distribution: 69 500–104 300).

distributions of these parameters for all five populations. For the parameters *N* and *R*, the priors are overlaid on the posteriors as thin lines. The mean, mode, standard deviation, and central 90% of these distributions are listed (Table 4). In addition, the sums of these quantities for *N* and *T* are shown. For *R*, the mean values are shown. These latter quantities were calculated in two ways: (*i*) as grand means of the individual population mean values and (*ii*) directly from the totals for *N* and *T*.

The posterior distribution of *N* and the distribution of *T* for all five populations are essentially normal. This is expected given the uniform priors employed. The shape of the distribution of *T* results from the uniform distributions for *U* and *M* employed in eq. 2. Given normal distribution of the data, the near-normality of binomial distributions for large sample size, and appropriately broad uniform priors on *R* and *N*, near-normality in the posterior of *N* is expected. In all five cases, the posterior is shrunk considerably from the lower and upper limits of the uniform prior.

Fig. 4. Fish-per-accessible-stream-kilometre for recent average and estimated 1895 abundance of Puget Sound steelhead. Black bars: recent 25-year average; open bars: recent 5-year average; grey bars: 1895 posterior mode; hatched bars: 1895 posterior 5th percentile.



analysis, however, we view this as a strength because it indicates that the severe reduction in the abundance of Puget Sound steelhead must be due primarily to a loss of capacity of the available habitat. This loss may reduce the carrying capacity of freshwater habitat directly through loss of suitable habitat or indirectly through changes in conditions that affect population productivity (via affecting growth and survival of early life stages). It remains to be determined to what extent this loss of productivity is due to changes in the physical and ecological conditions of freshwater habitat and which components of the steelhead life cycle may be most affected.

To provide further perspective on these estimates, we considered data for steelhead in the Situk River in southeast Alaska. Specifically, we examined data from 1952 based on weir counts that constituted a near-complete enumeration of the 1952 steelhead run (Bain et al. 2003). This run occurred at the end of a period of 12–15 years of rebuilding (two to three generations) that followed the cessation of efforts directed at eradicating steelhead in the Situk. During this rebuilding period, sport fishing and incidental commercial harvest was minimal (estimated annual harvest rate less than 8%), and spawning and rearing habitat conditions were as close to undisturbed as any stream or river in North America in the 20th century for which comparable data exists. The estimated run size ranges between 25 000 and 30 000 for the Situk at that time (Bain et al. 2003), and the best estimate of total stream kilometres accessible to adult steelhead is 100 km (Thedinga et al. 1993; B. Marsten, Yakutat Area Fish Biologist, Alaska Department of Fish and Game, P.O. Box 49, Yakutat, AK 99689, USA, personal communication 2009). This results in a range for FKM of 250–300, a range of values substantially greater than any of the values from our estimates for Puget Sound rivers in 1895, all of which are less than 150 FKM (Fig. 5).

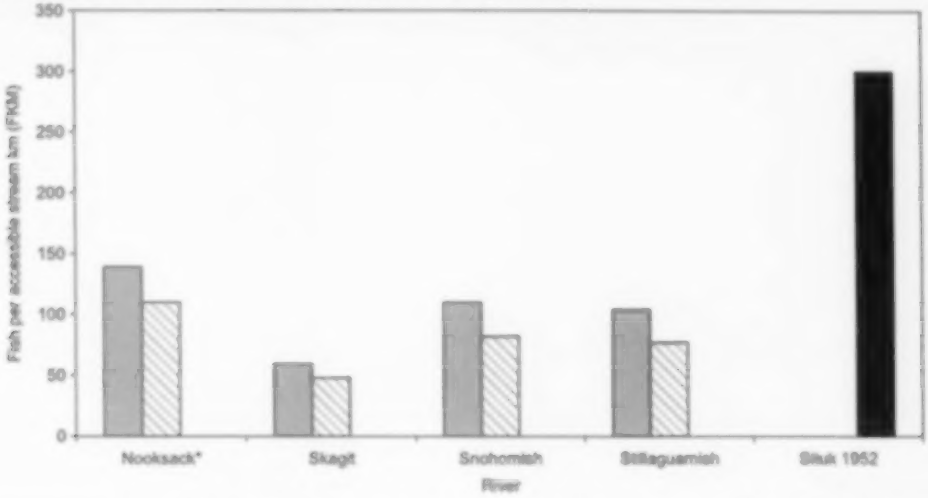
The Situk is a low-gradient, lake-controlled tundra river and might thus be thought to be unrepresentative of the productive potential of Puget Sound rivers. However, while it is clearly geomorphically different than most streams and rivers in the Puget Sound lowlands, it is arguably more relevant to the consideration of the inherent productive potential for steelhead of Puget Sound rivers than might first appear. The majority of large rivers in Puget Sound prior to being modified by Euro-American activities had extensive low-gradient floodplains with heavy loadings of large wood, braided channels, and vast wetlands (e.g., Bancroft 1890; Collins and Sheikh 2004; and Collins 2008) that created complex, low-gradient riverine habitats with rearing and spawning conditions that were likely not much different from the Situk. Given these historic conditions, we suggest that the Situk data provides a helpful perspective on the FKM values for Puget Sound that are associated with our 1895 estimates.

Potential importance of marine survival between periods

We have not speculated on possible differences in juvenile steelhead survival in the ocean between the period affecting the recruitment of the 1895 steelhead run and the period between 1980 and 2004. There are several reasons for this. First, we believe it unlikely that the 25-fold difference in abundance between the two periods that we have estimated could be accounted for primarily by differences in ocean survival. Differences in stock-specific smolt-to-adult survival of steelhead over a 20- to 30-year time span that have been recorded appear to be on the order of fourfold (Ward 2000). But even a 10-fold difference would not account for the discrepancy we have identified.

In this connection, it is relevant to note that early ocean survival of steelhead does not appear to exhibit as strong or as consistent a correlation with indices of ocean productivity such as the Pacific Decadal Oscillation (PDO) as do coho salmon *Oncorhynchus kisutch*. Second, to the extent that ocean survival of steelhead does follow the pattern of coho, it is of interest to note that the ocean conditions in the decade leading up to the 1895 Puget Sound steelhead run as indexed by the PDO appear to have been unfavorable. Biondi

Fig. 5. Fish-per-accessible-stream-kilometre for four major Puget Sound rivers estimated 1895 abundance and for Alaska's Situk River in 1952. Grey bars: 1895 posterior mode; hatched bars: 1895 posterior 5th percentile.



et al. (2001) reconstructed the PDO from 1991 back to 1661 based on the analysis of tree rings (dendrochronology) of bigcone Douglas-fir (*Pseudotsuga macrocarpa*) and Jeffrey pine (*Pinus jeffreyi*) from sites in southern California and northwestern Mexico. The reconstructed series correlated well with the PDO calculated directly by Mantua et al. (1997) for the period between 1900 and 1991 (correlation coefficient = 0.49, $P < 0.001$). A subsequent analysis of five published proxy records of North Pacific climate variability, including the Biondi et al. (2001) study, arrived at similar conclusions (Gedalof et al. (2002). During the decade from 1885 to 1894 that spans the period of juvenile recruitment to the 1895 adult run, the reconstructed PDO of Biondi et al. (2001) was consistently positive. A positive PDO correlated with poor ocean survival conditions for juvenile salmonids from southern British Columbia (Hare et al. 1999). The reconstructed series was also positive from 1977 to 1989 in accordance with the PDO as reported by Mantua et al. (1997), and which spans the first half of the 1980 to 2004 period. This suggests, but of course does not prove, that ocean conditions affecting steelhead recruitment to the 1895 run were not hugely different from those experienced in the recent past.

Differences between our estimate and that of Hard et al. (2007)

Our historical run size estimate is considerably larger than the 327 522 to 545 997 fish estimate prepared by Hard et al. (2007) for NOAA Fisheries' most recent status review of Puget Sound steelhead, even though both estimates are based on the same 1895 commercial harvest data set. There are two essential reasons for this. First, Hard et al. (2007) assumed that the average Puget Sound steelhead weighed 5.4 kg (12 lb) based on a reported average size range of 3.6 kg (8 lb) to 6.8 kg (15 lb), with an extreme of 11.3 kg (25 lb) (Rathbun 1900). Our deeper analysis of the available historical evidence indicated that this average mass was too high and should most likely lie within the bounds of 3.2 kg (7 lb) and 4.3 kg (9.5 lb). Second, we argue that the unreported catch of winter steelhead was much larger than Hard et al. (2007) suspected. Our analysis of available historical information indicated that the recorded commercial catch of steelhead likely only represented between one-half and two-thirds the actual catch in river basins where Native American subsistence fishing took place and also where agriculture was a dominant Euro-American settlement activity. Accordingly, we argue that the total harvest rates on the runs were likely to have been much higher than Hard et al. (2007) assume.

With regard to Euro-American settlement activity, our historical research revealed that staggering numbers of salmon and steelhead were speared, pitch-forked, snagged, and trapped at virtually every tributary, rill, and brook at spawning times by settlers who used the fish by the wagonload for fertilizer and livestock feed (Local Committee of Pioneers 1906; Jeffcott 1949; Edson 1968). The need for fertilizer was likely linked to the low soil nutrient levels in river valley areas previously forested with old growth trees. Clark (1970, p. 35) explains that the denuded forest soil was "acidic, sandy, and lean in minerals, good for fir and cedar but terrible for food crops. Without fertilizers which few people could obtain, it might yield at best a few grubby vegetables when cultivated with prayer and desperation." However, fertilizer was readily at hand in the streams, and settlers quickly learned to use the abundant spawning runs of anadromous fish (salmon in fall and steelhead in winter–spring) to build soil productivity prior to each planting.

Although Native American subsistence fishing was much reduced by 1895 from levels that occurred prior to Euro-American settlement, the schedule of this activity was much the same: salmon in the fall and steelhead in winter and spring. The rather considerable body of anthropological and ethnohistorical literature available for the Puget Sound region makes it clear that Puget Sound tribes did capture and utilize winter steelhead, and indeed these fish were prized by the Indians (e.g., Stern 1934; Smith 1940; Suttles 1974), even though much time was also spent in the longhouses in

winter engaged in story-telling, ceremonies, and feasting (Schalk 1977).

Historical commercial run-up to 1895 data set and the 70–30 split

It is worth noting that the 1895 commercial catch for the "remainder of Puget Sound" represents only 27% of the total, yet includes several large rivers in central and south Puget Sound: the Green, Puyallup, and Nisqually. Whether or not these rivers in particular had been heavily commercially fished prior to the late 1890s is difficult to determine from the available historical record. Puget Sound commercial fishing began more than 40 years prior to 1895 (1853), with increasing layers of commercial, subsistence, and agricultural harvests that went unrecorded until record keeping began in 1889. The pattern of development of settlement and commerce that included fishing moved predominately in a south-to-north direction. Commercial fishing in particular necessitated the arrival of railroads, which also developed in a south-to-north direction in conjunction with population growth. By 1890, the two Seattle–Tacoma area counties had a total population of 115 000 people, whereas the most populated north Puget Sound county had less than 19 000. Seattle and Tacoma were the major early fishing centers that peaked prior to any record keeping. By 1895, Tacoma was no longer even considered a fishing center. Consequently, for whatever reason, by 1895 the contribution of the large central and south Puget Sound rivers to the commercial steelhead catch was considerably smaller than the four large northern rivers. This is another reason that our estimate of the total Puget Sound run size in 1895 is conservative and under-represents the historic productive potential of Puget Sound rivers.

Relevance for recovery planning

The magnitude of the decline identified by our estimates of 1895 run sizes appears well out of proportion to the loss of habitat available to steelhead, as measured by our rough metric for habitat quantity. There is a considerable amount of stream habitat throughout Puget Sound that remains accessible to adult steelhead. Yet for reasons that remain to be identified or understood, the available habitat lacks either the capacity to hold the numbers of juveniles that it did around the turn of the 20th century or the conditions that enabled it to produce large numbers of healthy individuals that would survive to outmigrate as smolts.

Recovery planning for Puget Sound steelhead will need to identify and evaluate credible hypotheses about the causes of the severe decline in habitat capacity and productivity that is identified by our estimates of turn-of-the-20th-century abundance. Assessment of this loss is necessary to identify appropriate abundance targets for recovery that will insure the persistence of a delisted ESU. Clearly, there have been numerous changes to the environment occupied by Puget Sound steelhead as well as to the fish themselves. Interactions with hatchery conspecifics, reduction in the magnitude of runs of Pacific salmon, and simplification of life history components such as reduction or elimination of repeat spawning, in addition to possible changes in the magnitude and (or) pattern of marine survival, are all likely contributors that will have to factor into a comprehensive understanding of the decline in overall abundance that our analysis has indicated. There is some cause for optimism here in that the comparatively small amount of physical stream habitat lost over the past century relative to the magnitude of population decline suggests that recovering substantially larger wild population sizes may clearly still be in the cards.

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Appendix A

For the equation used to calculate the binomial likelihood (eq. 1), we begin by stating full factorial version of the binomial likelihood:

$$P(T|N,R) = \frac{N!}{T!(N-T)!} \cdot T^{R} \cdot (N-T)^{(1-R)} \quad \text{(A.1)}$$

where $T = C(1 + U)/M$, C is the reported 1895 commercial catch in pounds, U is a value for the unreported catch (in pounds) as a proportion of the reported commercial catch drawn randomly from the prior distribution of U, and M is a value for the average mass of steelhead in the run drawn randomly from the prior distribution of U.

In SWL, the likelihood is calculated in natural log space (ALOG). Equation A.1 must therefore be translated into natural log space. This requires the use of the logarithm of the gamma function (LGAM) to handle the factorials. We define the following:

$$\begin{aligned} \mathrm{FN} &= N + 1.0 \\ \mathrm{FT} &= T + 1.0 \\ \mathrm{FF} &= \mathrm{FN} - \mathrm{FT} + 1.0 \end{aligned}$$

$$\begin{aligned} \mathrm{GN} &= \mathrm{LGAM}(\mathrm{FN}) \\ \mathrm{GT} &= \mathrm{LGAM}(\mathrm{FT}) \\ \mathrm{GF} &= \mathrm{LGAM}(\mathrm{FF}) \end{aligned}$$

The log-likelihood is then calculated from

$$(\mathrm{GT} - \mathrm{GT} - \mathrm{GF}) + T \cdot \mathrm{ALOG}(R) + (N - T) \times \mathrm{ALOG}(1 - R) \quad \text{(A.2)}$$

As described in the text, eq. A.2 is calculated for each of 10 000 000 sets of random values sampled from the prior distributions of N, R, U, and M, and each set is then weighted by the likelihood value calculated for the set. Histograms and posterior summaries of selected parameters of interest are derived from these weights. Derived parameters, such as T, are also derived from these weights in a straightforward way (T, for example, using eq. 2 as explained in the text).

Reduced recruitment performance in natural populations of anadromous salmonids associated with hatchery-reared fish

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Abstract: We found a negative relationship between the reproductive performance in natural, anadromous populations of steelhead trout (*Oncorhynchus mykiss*), coho salmon (*O. kisutch*), and Chinook salmon (*O. tshawytscha*), and the proportion of hatchery fish in the spawning population. We used intrinsic productivity as estimated from fitting a variety of recruitment models to abundance data for each population as our indicator of reproductive performance. The magnitude of this negative relationship is such that we predict the recruitment performance for a population composed entirely of hatchery fish would be 0.128 of that for a population composed entirely of wild fish. The effect of hatchery fish on reproductive performance was the same among all three species. Further, the impact of hatchery fish from "wild type" hatchery broodstocks was no less adverse than hatchery fish from traditional, domesticated broodstocks. We also found no support for the hypothesis that a population's reproductive performance was affected by the length of exposure to hatchery fish. In most cases, measures that minimize the interactions between wild and hatchery fish will be the best long-term conservation strategy for wild populations.

Résumé : Nous observons une relation négative entre la performance reproductive de populations naturelles de truites arc-en-ciel anadromes (*Oncorhynchus mykiss*), de saumons coho (*O. kisutch*) et de saumons chinook (*O. tshawytscha*) et la proportion de poissons de pisciculture dans les populations de reproducteurs. Nous utilisons la productivité intrinsèque estimée en ajustant une variété de modèles de recrutement aux données d'abondance de chaque population comme indice de performance reproductive. L'importance de cette relation négative est telle que nous prédisons que la performance du recrutement dans une population composée entièrement de poissons de pisciculture serait de 0,128 celle d'une population composée totalement de poissons sauvages. L'effet des poissons de pisciculture est le même chez les trois espèces. De plus, l'impact des poissons de pisciculture provenant de stocks reproducteurs de pisciculture de « type sauvage » n'est pas moins négatif que celui des poissons de pisciculture de stocks reproducteurs traditionnels et domestiqués. Nous ne trouvons aucun appui à l'hypothèse qui veut que la performance reproductive d'une population soit affectée par la durée de son exposition aux poissons de pisciculture. Dans la plupart des cas, les mesures qui minimisent les interactions entre les poissons sauvages et les poissons de pisciculture constituent la meilleure stratégie de conservation à long terme pour les populations sauvages.

[Traduit par la Rédaction]

Introduction

The conservation of indigenous fish species throughout the world is commonly intertwined with artificial propagation programs (Fleming and Petersson 2001; Morita et al. 2006; McClure et al. 2008). This is particularly the case for anadromous salmonids in the US Pacific Northwest. Not only are fish reared for a portion of their life in a hatchery environment (hatchery fish), a nearly ubiquitous feature of this landscape, but naturally produced fish (wild fish), some of which are offspring of naturally spawning hatchery fish, are at risk and managed under the US Endangered Species Act (ESA) as threatened or endangered species (Ruckelshaus et al. 2002; Kostow 2009). In most instances, propagation of fishes has been intended to provide fish for consumption. However, in recent years the role of hatcheries has expanded to include the production of fish for conservation purposes.

Salmon and steelhead hatcheries in the US Pacific Northwest most commonly produce and release juvenile, ocean-migrating smolts. After reaching the ocean, these fish remain in the marine environment until they are mature. Upon maturity, they migrate back to their stream of origin to spawn. Although most artificially propagated fish are released directly from a hatchery into a local river basin, in some cases juvenile fish are transported to another, sometimes distant, location for release. The founding source for most hatchery broodstocks are wild fish captured from the same basin as where the hatchery is located. However, hatcheries may also obtain their initial broodstock via trans-

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fer of fish from other out-of-basin hatchery programs. In either case, once established, the stock's lineage is typically maintained by using hatchery adults returning to the basin where the hatchery is located. In recent years, the operation of many hatchery programs in the Pacific Northwest has changed, and now they purposefully capture and obtain wild adults each year to include as a portion of the broodstock. The incorporation of wild fish into hatchery broodstocks has been undertaken with the expectation it will ensure that the hatchery fish produced will be genetically similar to the local wild fish. Therefore, it is assumed that such genetically similar hatchery fish, if they escape capture and spawn in the natural habitat, will not harm, and may in fact benefit the conservation of the wild population.

The extent to which hatchery fish are an impediment or benefit to the recovery of Pacific salmon and anadromous trout (*Oncorhynchus* spp.) remains a question of much importance and debate (ISAB 2003; Brannon et al. 2004). Plans developed to conserve and recover such species must accurately address the issue of artificial propagation if they are to succeed, given the widespread distribution of hatchery fish in this region. However, this is a difficult proposition, because the empirical basis for understanding the issue is limited and heavily biased to a single species, steelhead trout (Berejikian and Ford 2004; Araki et al. 2008). From the studies completed to date, it appears that when the focus of the question is genetic or ecological, the most common assessment is that hatchery fish pose a risk to wild fish (ISAB 2003; Kostow 2009). However, the reproductive support provided by naturally spawning hatchery fish may help conserve populations of wild fish (Saisa et al. 2003; Sharma et al. 2006; McClure et al. 2008). Therefore, when it comes to the effect of hatchery fish, there seems to be a shifting balance between risk and benefit, depending on the conservation issue focused upon. We believe that this contributes to the diversity of the findings reported. In addition, it is likely that these divergent conclusions are also related to study-specific dissimilarities such as, which species was evaluated, the magnitude of genetic dissimilarity between the hatchery and wild population, issues of habitat or genetic legacy, and study methodology.

Given these complexities, coming to an overarching assessment of the impact of hatchery fish on wild populations remains a challenge. However, we believe that our methods and results may shed some light on this task. We expand on an approach first described by Chilcote (2003) and Nickelson (2003) that evaluates whether natural populations with a high frequency of hatchery fish have the same recruitment performance, in terms of offspring produced per parent, as those populations where the frequency of hatchery fish is low. We note that a critical element of such an approach is the demonstration that the relation between hatchery fish and recruitment performance is not confounded by other, unrelated factors. This methodology originated with the supposition that if the lower reproductive success of hatchery fish reported by Chilcote et al. (1986), Leider et al. (1990), and McLean et al. (2003) was generally true, then the recruitment performance of naturally reproducing populations should vary directly with the proportion of the spawners that were hatchery fish. We expect that in addition to the genetics-based effects of hatchery fish, variations in recruitment performance should reflect the effects of ecological interactions between hatchery and wild fish as well. We report here on the results of an investigation that examines the effect of hatchery fish on the recruitment performance of naturally reproducing populations of anadromous salmonids occurring across a relatively large and environmentally diverse geographic area. We note that while the focus here is salmonid and regional, we believe our findings are relevant to conservation of a wide range of species and environments where artificial propagation is a consideration.

Materials and methods

Overview

Our study focuses on assessing how much of the variation in recruitment performance among different populations can be explained by differences in the proportion of hatchery fish (P_h) in the spawning population. To accomplish this we performed an analysis of covariance (ANCOVA) to isolate the possible effect of (P_h) from several other, potentially confounding factors with respect to the response variable, intrinsic productivity. Intrinsic productivity is a population recruitment performance metric defined as the number of offspring produced (recruits) per parent (spawner) at very low spawner densities. We estimated this metric by fitting a variety of different recruitment models to approximately 20 brood years of parent and progeny abundance data for each population we analyzed (see supplementary data,[2] Table S1). We emphasize that by standardizing our estimate of recruits per spawner to near zero spawner abundance levels (intrinsic productivity), we intended to shield our productivity estimates against the confounding effect of density dependence, which arises from the data set variations in spawner abundance relative to habitat capacity.

Study sites

For our evaluation, we selected 93 populations of anadromous salmonids from the states of Oregon, Washington, and Idaho, USA, that were known to contain both wild and hatchery fish. Three species were represented: steelhead trout (*Oncorhynchus mykiss*), coho salmon (*O. kisutch*), and Chinook salmon (*O. tshawytscha*). On the basis of run-timing, steelhead populations are classified as either being winter-run or summer-run. Likewise for Chinook, two groups are identified, fall Chinook and spring Chinook. Our sampling, in general, reflected the current distribution of these species within the study area (Fig. 1). However, because of the lack of sufficient population abundance and hatchery data, we excluded portions of western Washington from our sampling area. In addition, the lack of sufficient data resulted in an under-representation of steelhead populations from the Oregon coast and upper Snake regions (Table 1). The majority of Chinook and steelhead populations (21 of 35 and 22 of 32, respectively) were from the Columbia River basin. In contrast, nearly all of the coho populations (24 of 26) were from coastal basins.

[2] Supplementary data for this article are available on the journal Web site (http://cjfas.nrc.ca).

Fig. 1. Map of the study area showing locations of population sampling regions, data sites used to construct for low average air temperature index (LAAT, open circle, ○), and data sites for maximum snow depth index (MSD, open triangle △). Inset shows location in Pacific Northwest, USA.

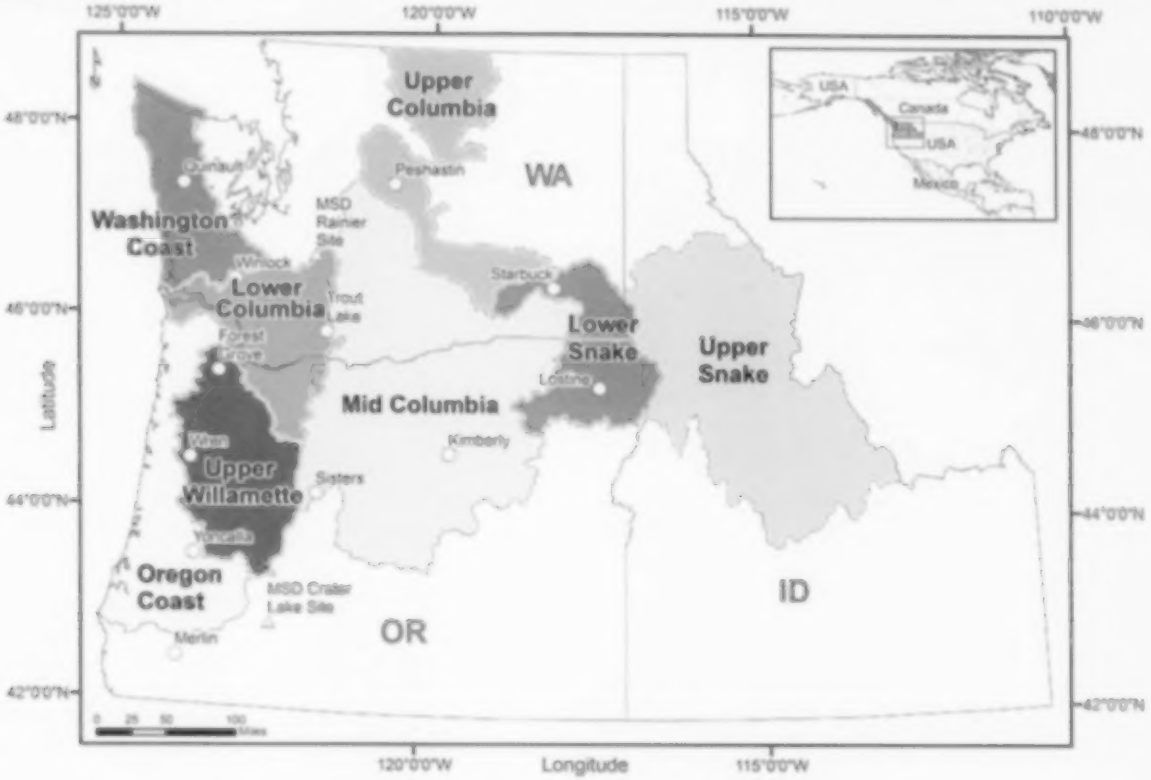


Table 1. Number of anadromous trout (winter steelhead and summer steelhead) and salmon (fall Chinook, spring Chinook, and coho) populations sampled from eight study regions, as illustrated in Fig. 1.

	Anadromous trout		Salmon		
Region	Winter steelhead	Summer steelhead	Coho	Fall Chinook	Spring Chinook
Oregon Coast	2	3	17	2	3
Washington Coast	5	0	7	6	3
Lower Columbia	4	3	2	2	2
Upper Willamette	3	—	—	—	1
Mid-Columbia	—	6	—	0	1
Upper Columbia	—	3	—	0	3
Lower Snake	—	3	—	0	7
Upper Snake	—	0	—	—	5

Note: —, denotes no populations sampled because region is currently not part of the species range.

Parental abundance

Annual estimates from 1981 to 2000 of parental (spawner) abundance for each population were based on information sources that differed by species and region. For the Oregon Coast, Washington Coast, and lower Columbia regions, we relied on coho abundance data provided by Wainwright et al. (2008), PFMC (2009), and McElhany et al. (2007), respectively. For Oregon Coast populations of steelhead, we utilized information presented by Chilcote (2003), updated to include data for the most recent years. Steelhead data for the lower Columbia and upper Willamette regions were obtained from McElhany et al. (2007). For the steelhead populations from mid-Columbia and lower Snake regions we relied on information presented by Chilcote (2003) and Carmichael and Taylor (2009). For the Oregon Coast populations of fall Chinook, spawner abundance esti-

mates were based on unpublished information provided by B. Riggers (Oregon Department of Fish and Wildlife (ODFW), Corvallis, Oregon, USA). Washington Coast fall Chinook abundance estimates were based on information provided by PFMC (2009). For spring Chinook, spawner abundance estimates were derived for the Oregon Coast, Washington Coast, and lower Columbia populations from unpublished information provided by K. Goodson (ODFW, Salem, Oregon, USA), PSC (2008), and McElhany et al. (2007), respectively. For the mid-Columbia region, spring Chinook estimates were based on information provided by Lindsay et al. (1985), Olson and Spateholts (2001) and Gauvin et al. (2007). For the remaining regions (upper Columbia, lower Snake, and upper Snake), we utilized population abundance information reported by the ICTRT (2008).

Proportion of hatchery fish

We estimated the proportion of hatchery fish in the natural spawning population (P_h) for each data series from spawner abundance estimate data as the unweighted mean of annual P_h values. In general the method used to classify hatchery and wild fish was similar to the approach reported by Chilcote (2003), which was based on the observation of marked hatchery fish or the resolution of hatchery growth patterns from the analysis of scales taken from a sample of the spawners (Scarnecchia and Wagner 1980). In some instances, the P_h estimate for a particular year was missing from the data set. In these cases, we averaged the P_h values for the year before and year after the missing data point to estimate its value. P_h data for the Sandy spring Chinook population and for fall Chinook belonging to the Sandy, Clatskanie, and Hoko populations, there were too many missing values from the time series to apply this method. Our alternative in these four instances was to estimate annual P_h values as the average of those years in the data set with P_h values.

Progeny abundance

We estimated the preharvest number of adult progeny (recruits) naturally produced by each brood year of spawners using the following four-step process. First, we estimated annual return abundance by dividing the fishery survival rate, calculated as 1 − fishery mortality rate, into the observed number of wild spawners. Next, we split each return into age categories, on the basis of the assumed proportion of different age at maturity for each population. A table of return estimates by each age category was then constructed, and members produced by each brood year were identified. Finally, all members of each brood year were totaled to yield an estimate of recruits. This procedure was modified for coastal and lower Columbia populations of Chinook because of their multiyear exposure to ocean fisheries. For these populations the order of steps used to estimate recruits was changed such that the adjustment for fishery impact was the last step rather than the first. In these cases, we used fishery impact rates estimated by brood year rather than by run-year as for the other populations.

Adult age data were generally obtained from the same source as the adult abundance data. However, we also drew on age composition information reported by Myers et al. (1998) for Chinook and Busby et al. (1996) for steelhead. For each population we accumulated all of the age information, which in most cases was less than five sample years, and calculated a single, unweighted estimate of the proportion of each age at maturity. We acknowledge this approach is inferior to having sufficient age data, such that an independent estimate of age composition can be made for each year in the data set. For example, Zabel and Levin (2002) report that when recruitment models are fit to data sets where estimates of recruits have relied on a single, averaged age composition there is a risk of model parameter bias. However, given that this is not a problem in the case of coho salmon (all adults are the same age) and that annual age composition data was rare for the steelhead and Chinook data sets, we believe our approach was the appropriate solution to an inherent short-coming of the information available to us. We also note that Schaller et al. (2000) concluded that the effect of imposing a constant age structure on a population data set, as we have essentially done, made only very small changes in the values for intrinsic productivity estimated from recruitment model fitting.

Annual estimates of past fishery impact rates for steelhead were based on an updated version of information described by Chilcote (2003) and McElhany et al. (2007) for Oregon populations, and by Scott and Gill (2008) for Washington populations. Annual fishery impact rates for Oregon coho populations were provided by Chilcote et al. (2005) and McElhany et al. (2007). For Washington coho, fishery impact estimates were developed from unpublished fishery catch data (J. Haymes, Washington Department of Fish and Wildlife, Olympia, Washington, USA, personal communication 2009).

Ocean fishery impact rates used for Oregon and Washington coast fall Chinook populations were those reported by PSC (2008). Terminal (non-ocean) fisheries exist for nearly all of these populations as well, and the associated impact rates we used were also those provided by PSC (2008). We used both the ocean and terminal fishery impacts in our calculation of pre-fishery recruits for these populations.

For interior Chinook populations of Oregon, Washington, and Idaho, which are rarely caught in ocean fisheries (Myers et al. 1998), the primary fishery impacts are within the Columbia River. We estimated impact rates for these fisheries from escapement and run-size information for the Columbia upriver spring Chinook described by PSC (2008). For upper Willamette and lower Columbia spring Chinook populations, we used brood year impact rates for the upper Willamette indicator stock (PSC 2008). For spring Chinook belonging to the south coast Oregon grouping, we used the brood year exploitation rates for Rogue River Chinook described by ODFW (2007). For spring Chinook populations from the northerly portion of the Oregon Coast, we used the same impact rates as those for fall Chinook populations. For Washington coast populations of spring Chinook, we estimated brood year total fishery impacts by averaging the total exploitation rates for the upper Willamette and Skagit indicator stocks described in PSC (2008).

Environmental variables

We included one of four possible environmental indices in all recruitment models as an additional predictor variable in an attempt to account for some of the variability in both

freshwater and marine conditions. These indices were: maximum snow depth (MSD), Columbia River flow (CRF), spring Pacific decadal oscillation (SPDO), and low average air temperature (LAAT). We selected these particular environmental indices because they represent elements of the natural environment that may have a strong effect on salmon and steelhead, specifically: mountain snowpack, river flow, air temperature, and ocean conditions. There is also good evidence that these elements are sensitive to large scale climatic shifts that effect salmon populations in the Pacific Northwest (Mote et al. 2003). These indices were standardized to the 1917 to 2007 period by subtracting annual measurements from the data series mean and then dividing the result by the standard deviation of the data series (see supplementary data,[2] Table S2) . The snow index (MSD) is derived from snow depth measurements (NCDC 2009) for the Paradise survey site within Mt. Rainier National Park and the Headquarters survey site within Crater Lake National Park (Fig. 1). We averaged the annual maximum snow depth recorded for each of these locations to generate the MSD index. The Crater Lake and Mt. Rainier survey sites are unique in that the data series starts earlier (1917) than any other mountainous location within our study area. These sites also are likely representative of the two primary patterns of temporal variation in snowfall in the Pacific Northwest (Peterson and Peterson 2001). We developed the SPDO index by averaging April, May, and June values for the Pacific decadal oscillation (PDO) index as reported by JISAO (2009). The PDO index is derived from sea surface temperature anomalies in the North Pacific Ocean (Mantua et al. 1997). The CRF index was based on the annual average discharge estimates for the Columbia River measured at The Dalles dam (USGS 2009). The LAAT index was developed from regional air temperature data (PRISM Climate Group 2009) for 12 locations corresponding with the town sites of Quinault, Winlock, Peshastin, Trout Lake, Starbuck, Forest Grove, Wren, Yoncalla, Merlin, Sisters, Kimberly, and Lostine (Fig. 1). All sites were less than 1000 m a.s.l. and distant from large metropolitan areas. The LAAT index represents an average of the standardized index values for all 12 locations.

Recruitment models

We used the Ricker recruitment function as the basis for our recruitment models (Ricker 1954), described here by $R_t = \alpha S_t \exp(-\beta S_t)$, where S_t is the total number of spawners (hatchery plus wild fish) in year t; R_t is the number of natural recruits that were produced by the fish that spawned in year t; α is the model parameter for intrinsic productivity; and β is the model parameter that represents the strength of the density dependent relationship with spawner abundance. We modified this basic equation in two ways. First, we incorporated annually-based environmental indices with a parameter represented by γ. Second, we transformed the equation to the lognormal form to clarify that we assumed a lognormal error structure. The resulting equation was as follows:

$$(1) \qquad \ln(R_t) = \ln(S_t) + \ln(\alpha) - \beta S_t + \gamma E_{it+\text{lag}}$$

where E_i is the index value for the environmental variable where i = 1–4 for MSD, SPDO, CRF, and LAAT, respectively, and with each index value having a reference year equal to t+lag, where lag may assume a value from –2 to +2 years. Our rationale for considering different time lags for the environmental variable was that we were uncertain both about the primary life history stage affected by the index, and the delay between quantitative shifts in environmental variable and the biological response, in terms of conditions that effect salmon and steelhead survival.

For each population, we considered 20 different recruitment models as specified using all possible combinations of four environmental variables and five different lag periods. We attempted to fit each of these models to the associated spawner, recruit, and environmental index data sets via multiple nonlinear regression using the DataFit software developed by Oakdale Engineering (Oakdale, Pennsylvania). To eliminate biologically unrealistic solutions, we rejected models that yielded α parameter estimates > 30 and those solutions for α and β that yielded a maximum possible recruits value that was >10× the mean observed number of population recruits. For those models not rejected, we calculated scores for the corrected Akaike's information criterion (AICc) (Burnham and Anderson 2002) and ranked them accordingly. We then selected the top-ranked models that cumulatively represented 95% of the AIC weight. From this subset of candidate models we then re-standardized the weights and computed a weighted average value for the $\ln\alpha$ parameter using the AICc weights based on

$$(2) \qquad \ln\alpha_{\text{estimate}} = \sum(\ln\alpha_i \times \text{AICc wt}_i)$$

where $\ln\alpha_i$ is the parameter estimate for i_{th} model, and AICc wt_i is the corresponding AICc weight.

We performed an assessment to determine whether our recruitment model selections of specific environmental variables or time lags were independent of the population value for P_{h}. We first performed an arcsin transformation of mean P_{h} values for each population. We then divided populations into four classes depending on the environmental variable selected in the best recruitment model for each population. Next, we performed an analysis of variance (ANOVA) test to determine whether the mean P_{h} values for each of these classes departed from the null hypothesis that they were equal. Time lags for the environmental index were evaluated in a similar fashion, except that since there were five possible time lags there were five classes to compare.

Covariates

The populations we evaluated contain hatchery fish from different types of programs. Using terminology described by USFWS (2010), we classified these as either being a segregated type (ST) or an integrated type (IT). We defined ST hatchery programs as those where local wild fish supplied less than 10% of each year's hatchery broodstock and IT hatchery programs, as those where local wild fish comprised from 10% to 100% of each year's broodstock. We assigned the ST classification to all hatchery fish that occurred in basins not associated with a dedicated hatchery program (i.e., they had strayed from other out-of-basin locations). Because it is likely IT hatchery fish are genetically more similar to wild fish than ST hatchery fish, we included hatchery type as a covariate in our models to assess whether the effect on

population recruitment performance was different between these two forms.

We included several other covariate variables in our analysis to determine whether the observed variation in $\ln\alpha$ can be explained by factors that may be confounded with P_{b}. We examined our data for evidence that hatcheries (and thereby higher P_{b} values) were more common in basins with poorer habitat quality. If hatchery programs were initiated mostly for basins having poor habitat and not those with good habitat, then it is possible any relation found between $\ln\alpha$ and P_{b} could be an artifact of a habitat–hatchery correlation. To examine this question, we added a variable to our models that indicates whether or not a hatchery was located in each population's basin. If hatcheries are located in basins with poor habitat where intrinsic productivity is generally suppressed, then we expect this factor to absorb a significant fraction of the observed variation in $\ln\alpha$. We also used this covariate to test a second question, which was whether the presence of an in-basin hatchery might cause a distortion in the distribution of naturally spawning hatchery fish sufficient to confound an independent measurement of intrinsic productivity. The concern was that because of innate homing behavior, an in-basin hatchery may provide such a strong attractor for returning hatchery fish that spawners might not distribute themselves throughout the basin. Rather, they could become concentrated in areas close to the hatchery where the habitat may be suboptimal and crowded with hatchery offspring. If this were to occur, then the net intrinsic productivity measured for the population (hatchery plus wild spawners) may be low owing to the distorted spawning distribution of hatchery fish, and not inherently low reproductive performance. The possibility that such a phenomenon exists is supported, if the intrinsic productivity of those populations that occur in basins where a hatchery is located is lower than for populations that occurred in basins without a hatchery.

The migration corridor to and from the ocean for many populations is impaired by the existence of large hydroelectric dams. A potentially confounding negative relation between $\ln\alpha$ and P_{b} could arise if P_{b} and the number of dams in the migration corridor is positively associated. We examined this question by including the number of dams within a basin as a potential predictor of $\ln\alpha$.

We also examined whether the length of time a population has been exposed to naturally spawning hatchery fish is related to intrinsic productivity. To do this, we assigned a classification for a hatchery legacy covariate depending on the years of exposure to hatchery fish as follows: short, less than 10 years; moderate, 11 to 20 years; and long, more than 20 years. We determined the exposure period by examining population data sets and additional information about hatchery program history.

Productivity models

We initially created an a priori list of 11 candidate models to weigh the various factors that might affect population productivity ($\ln\alpha$). Model 1, the most complex model (Table 2), contains all factors plus an interaction between P_{b} and species. In an attempt to refute the hypotheses that variation in $\ln\alpha$ is attributable to P_{b}, we developed Model 2 (Table 2), which is the same as the most complex model, except that terms for P_{b} and an interaction between P_{b} and species are removed. Four other models (Models 3–6) were created that do not contain terms with P_{b}, and lack one additional covariate. These four models also refute the hypothesis that variation in $\ln\alpha$ is attributable to P_{b}, and assume that one other covariate is unnecessary. We then created Models 7–10, which assume variation in $\ln\alpha$ is attributable to P_{b} (Table 2). These models are simpler than the full model, and therefore assume that some covariates are unnecessary. To examine the specific hypothesis that type of hatchery (ST versus IT) affects the relationship between $\ln\alpha$ and P_{b} we created Model 11 (Table 2).

The models in Table 2 contain both continuous and discrete predictors. Thus, we conducted an analysis of covariance (ANCOVA) with the *lm* function available in R, a statistical programming platform available online (R Development Core Team). We used the inverse of the standard error of estimates of $\ln\alpha$ as weights in the ANCOVA (Burnham and Anderson 2002). This allows factor levels associated with more precise estimates of $\ln\alpha$ to exert a greater influence on model fit than factor levels associated with greater uncertainty in $\ln\alpha$. We then used Bayesian Information Criterion (BIC) to compare model fits and identify a "best" model. Upon inspecting the ANOVA table for the best model among our initial list of 11 candidate models, we noted that the term for the interaction between P_{b} and species has the smallest sum of squares. We then decided to create a 12th model (Table 2, Model 12) that did not include a term for this interaction.

Results

We excluded 4 of the 93 populations from further analysis because were unable to successfully fit a recruitment model to the associated data set. This excluded group consisted of one steelhead trout population and three coho salmon populations. Although the estimates of $\ln\alpha$ were based on a weighted averaging of multiple recruitment models, we found that the best model for each population was dominant with an average AICc weight of 0.85 across all populations (see supplementary data,[2] Table S3). With respect to the best recruitment models, we found no evidence from our ANOVA analysis that the P_{b} values for populations having different environmental values or time lags were statistically dissimilar. The environmental index most commonly represented in the best model was CRF (40 populations). The occurrence of the other indices were less frequent with the MSD, LAAT, and SPDO indices represented in the best model for 25, 16, and 8 populations, respectively. The sign for the γ parameter was consistently positive for the MSD and CRF indices, indicating a positive relation with recruitment performance (Fig. 2). In contrast, for LAAT and SPDO a negative sign for the γ parameter was the norm, indicating these indices had an inverse relationship with recruitment performance.

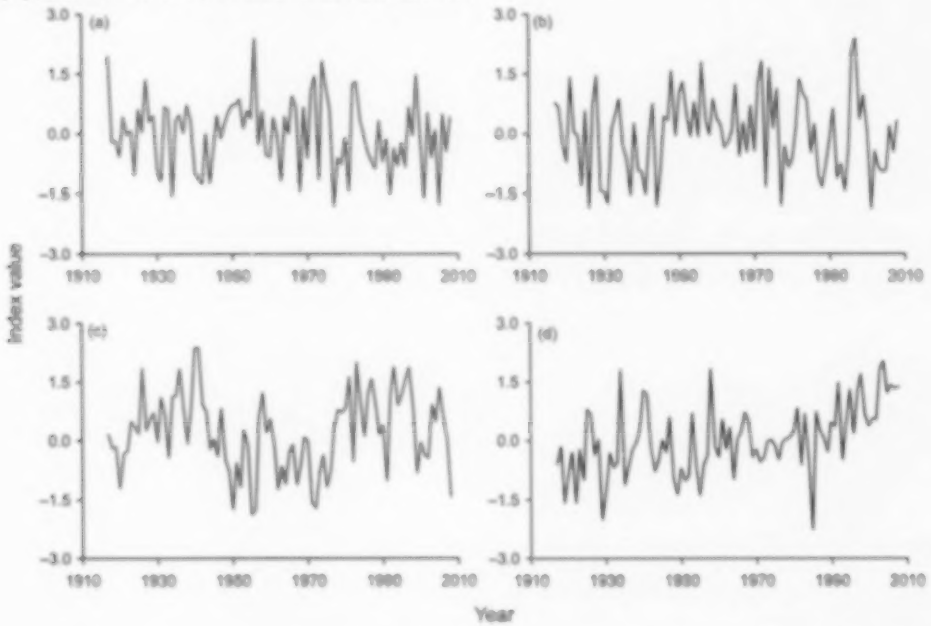
The median P_{b} value for the 89 populations to which we successfully fit a recruitment model to was 0.27, with values for the 10th and 90th percentiles of 0.02 and 0.71, respectively. The degree of annual variation in P_{b} values within data sets for individual populations was not large and consistent with relatively stable hatchery programs. However, for 13 populations the data sets included a period of no

Table 2. Productivity models considered to explain the variability in the natural logarithm of intrinsic productivity for 89 populations of Pacific Northwest salmon and steelhead.

ID	Productivity model	df	BIC	Rank
1	$\ln\alpha = P_h$ + Species + Hatchery type + Hatchery legacy + Hatchery location + Dams + P_h:Species	12	157.2	3
2	$\ln\alpha$ = Species + Hatchery type + Hatchery legacy + Hatchery location + Dams	9	215.3	9
3	$\ln\alpha$ = Species + Hatchery type + Hatchery legacy + Hatchery location	8	229.8	11
4	$\ln\alpha$ = Species + Hatchery legacy + Hatchery location + Dams	8	210.9	8
5	$\ln\alpha$ = Species + Hatchery type + Hatchery location + Dams	7	239.0	12
6	$\ln\alpha$ = Species + Hatchery type + Hatchery legacy + Dams	8	217.8	10
7	$\ln\alpha = P_h$ + Species + Hatchery type + Dams + P_h:Species	9	161.1	4
8	$\ln\alpha = P_h$ + Species + Hatchery legacy + Dams + P_h:Species	10	165.6	5
9	$\ln\alpha = P_h$ + Species + Hatchery location + Dams + P_h:Species	9	148.3	2
10	$\ln\alpha = P_h$ + Species + Hatchery type + Hatchery legacy + Hatchery location + P_h:Species	11	174.6	7
11	$\ln\alpha = P_h$ + Species + P_h:Hatchery type	6	170.0	6
12	$\ln\alpha = P_h$ + Species + Hatchery location + Dams	7	144.2	1

Note: Model 1 is the most complex model and it contains all observed factors plus one interaction; models 2–6 support the hypothesis that productivity is unrelated to proportion of hatchery-origin fish (P_h); Model 1 and models 7–12 support the hypothesis that P_h is an important predictor of productivity; the degrees of freedom (df), Bayesian Information Criterion (BIC), and rank of each model are provided.

Fig. 2. Temporal pattern of values for the environmental indices (*a*) maximum snow depth (MSD), (*b*) Columbia River flow (CRF), (*c*) spring Pacific decadal oscillation (SPDO), and (*d*) low average air temperature (LAAT) considered as variables in population recruitment modeling of 93 populations of coho and Chinook salmon and steelhead.



hatchery fish ($P_h = 0.0$) and a second period of many hatchery fish ($P_h > 0.4$), or the reverse. It is possible that using mean P_h to represent the cumulative effect of hatchery fish for such populations may lose important detail of the dynamics involved. However, if atypical dynamics do exist in these cases, we assume that our inclusion of a hatchery legacy covariate in our models would allow us to at least detect its existence, as most of these populations had an exposure period to hatchery fish of less than 10 years and therefore were classified as having a "short" hatchery legacy.

As evidenced by BIC scores, productivity models that did not contain P_h as a covariate were distinctly inferior to models that did (Table 2). The best productivity model (Model 12) contained terms for P_h, species, hatchery location, and dams. To assess whether this model meets the assumptions of ANCOVA, we inspected normal quantile-quantile plots, plots of residuals vs. fits, and residuals vs. leverage. These diagnostics yielded results strongly consistent with the major assumptions of this parametric test. The adjusted R^2 for the best productivity model was 0.72, and the sums of squares for P_h, species, hatchery location and dams were 41, 13, 2, and 7, respectively. So for example, P_h was nearly 3× more important than the next factor, species, in the model's accounting for the variation in $\ln\alpha$. Reversing the order in which terms are entered into the model had a very small affect on the distribution of sums of squares.

The slope of $\ln\alpha$ over P_h for the best model (Model 12) is –2.05 (Table 3). Thus, a naturally spawning population composed entirely of hatchery fish would have a reproductive performance rate that is $\exp(2.00 - 2.05)/\exp(2.00) = 0.128$ of that expected for a population composed entirely of wild fish. Since the best model does not contain a term for an interaction between P_h and species, this difference in productivity is identical for all three species. The intercept in Table 3 refers to $\ln\alpha$ for Chinook salmon with in-basin hatcheries and no dams in the migratory corridor. The $\ln\alpha$ for coho salmon is 0.02 less than the value for Chinook, which is statistically insignificant. However, for steelhead trout, the $\ln\alpha$ value is 0.66 less than for Chinook: a difference that is statistically significant (Table 3). Thus species differences effects the absolute value of $\ln\alpha$ at different levels of P_h, but the relative change from a population where $P_h = 0.0$ to one where $P_h = 1.0$ is the same (Fig. 3). The $\ln\alpha$ for fish in basins that do not have a hatchery is 0.36 less than the $\ln\alpha$ for fish in basins with a hatchery. This difference is also highly significant. Finally, $\ln\alpha$ declines by 0.07 with the addition of every dam to the migration corridor. The relation between $\ln\alpha$ and P_h changes if the population exists above dams, or if there is no hatchery located in the basin where it exists (illustrated in Fig. 4). However, as is the case with the species comparison, the relative rate at which productivity decreases with increases with P_h remains the same, even though the absolute level of $\ln\alpha$ predicted under these different dam and hatchery scenarios varies.

Finally, Model 11, representing the hypothesis that the slope of $\ln\alpha$ over P_h depends on hatchery type, was ranked as the 6th best productivity model (Table 2). Furthermore, the interaction term in Model 11 representing this hypothesis (i.e., hatchery type has an effect) explains just 0.005 of the observed variation in $\ln\alpha$, and is not statistically significant ($P = 0.27$).

Discussion

Our primary finding is that across a broad geographical range and three different species, P_h was a population characteristic that is negatively associated with reproductive performance. Intrinsic productivity declines as the fraction of the hatchery spawners in the natural population increases. We came to this conclusion after considering 12 different models that attempted to weigh the effect of four other covariates in addition to P_h. For our best model, we were able to account for 72% of the variation in the intrinsic productivity among the populations examined. The ability to explain this much of the variation, given the diversity of populations involved, leads us to believe our productivity model is quite robust. We found that although steelhead had lower $\ln\alpha$ values than coho and Chinook populations, within each species group, a naturally spawning population composed entirely of hatchery fish would have a reproductive performance that is 0.128 of that expected for a population composed entirely of wild fish.

This result was qualitatively consistent, at the individual species level, with those of Chilcote (2003) for 12 populations of Oregon steelhead, as well as the findings of Buhle et al. (2009) for 15 populations of Oregon coho salmon. In addition, the deficit in reproductive performance we predict for hatchery fish in our study (i.e., 0.128) is strikingly similar to values reported for the reproductive success of hatchery steelhead relative to wild steelhead of 0.129 by Leider et al. (1990) and 0.110 by McLean et al. (2003).

Berejikian and Ford (2004) report that the evidence for a natural reproductive performance difference between hatchery and wild fish falls disproportionately to studies of steelhead. They also caution that steelhead may be a poor representative of what might be expected for other salmon species in terms of reproductive performance of hatchery fish spawning in the wild. One reason for this view is that the normal hatchery rearing protocol for steelhead compresses the freshwater rearing period to one-half of what occurs in the wild. For coho and Chinook, the freshwater rearing period is not compressed in this manner, therefore the genetic selection for rapid growth in the hatchery environment presumably is not as intense, and the opportunity for fitness loss due to domestication is not as great. However, we find no evidence for a higher rate of domestication for hatchery steelhead as opposed to the other two species. Had such a difference existed, and the genetic change associated with this domestication process been proportional to the reproductive performance of hatchery fish spawning in the wild, then we would not have expected to find the relation between P_h and $\ln\alpha$ for steelhead to be essentially the same as that for coho and Chinook. In general, we conclude that steelhead may be no different than Chinook and coho in terms of being a representative species to study issues related to the reproductive performance of hatchery fish under natural conditions.

The hypothesis that hatcheries tend to be sited in basins where the habitat is most degraded, and therefore the populations less productive, was not supported. Indeed, our findings seem to support the opposite view, which is that less productive populations and presumably worse habitat conditions tend to be found in basins where hatcheries are not built. This result also refutes a related hypothesis that hatchery fish home with such fidelity to their natal hatchery that they do not disperse into the productive portions of the basin, and as a consequence, contribute poorly to natural production. For this hypothesis to be correct, populations associated with in-basin hatcheries should have lower reproductive performance. As noted already, we found the reverse to be true.

Surprisingly, we found that neither length of time exposed to hatchery fish nor hatchery type has any effect on a population's intrinsic productivity. Our best productivity models for explaining the observed variation in $\ln\alpha$ do not include either of these factors as covariates. With respect to the issue of hatchery legacy, there may be several explanations for our results. First, if the adverse effect of P_h on $\ln\alpha$ has a genetic basis, then perhaps a majority of the adverse effect accumulated faster in the population than we were able to detect. Alternatively, strong selection forces in the natural environment may purge maladapted genetic characteristics from the receiving wild population, and slow the accumulation rate of traits that impair reproductive performance such that it might take 30 or more years before the accumulation effect can be detected. Yet another alternative is that the effect of P_h we observe has an ecological, rather than a genetic basis, which was suggested by Nickelson (2003). If

Table 3. Parameter estimates, SE, and significance of the factors in the best productivity model (Model 12 in Table 2) for 89 populations of Pacific Northwest salmon and steelhead.

Factor	Estimate	SE	*t* value	Pr. (>|*t*|)
Intercept[a]	2.00	0.09	21.40	<0.001
P_h	–2.05	0.16	–12.63	<0.001
Species = coho	–0.02	0.13	–0.14	0.892
Species = steelhead	–0.66	0.10	–6.53	<0.001
Hatchery location = out	–0.36	0.09	–3.93	<0.001
Dams	–0.07	0.01	–5.19	<0.001

Note: Pr., probability.

[a]Intercept represents the baseline with Chinook salmon as the species, the presence of an in-basin hatchery, and no dams in the migration corridor.

Fig. 3. Relationship between mean proportion of hatchery fish in the spawning population (P_h) and intrinsic productivity expressed as recruits per spawner at near-zero spawner levels as predicted from the productivity model with the lowest Bayesian Information Criterion (BIC) score (Model 12) for Chinook salmon (open square, □), coho salmon (open triangle, △), and steelhead (filled circle, ●) under the assumption of no major dams in the pathway to the ocean and the presence of an in-basin hatchery.

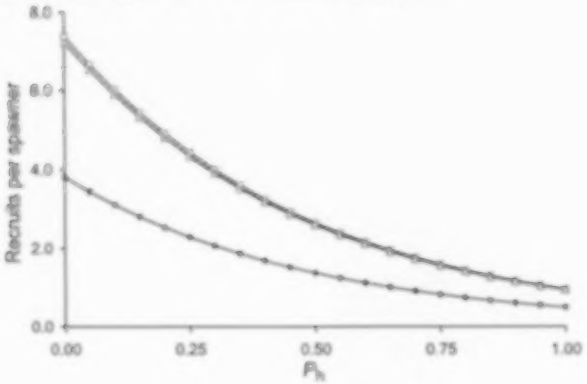
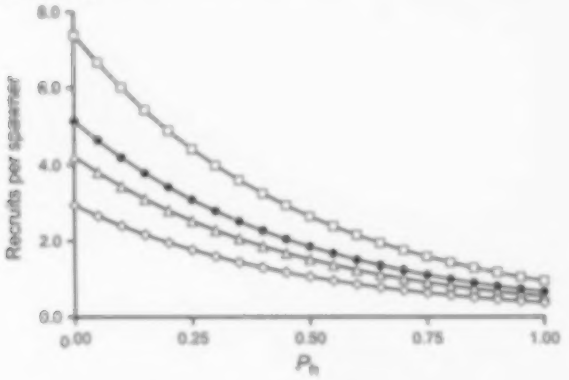


Fig. 4. Relationship between mean proportion of hatchery fish in the spawning population (P_h) and intrinsic productivity expressed as recruits per spawner at near-zero spawner levels as predicted from the productivity model with the lowest Bayesian Information Criterion (BIC) score (Model 12) for Chinook salmon under a range of different conditions including the base condition of no dams and an in-basin hatchery (open square, □), no in-basin hatchery (filled circle, ●), eight dams in the migration corridor (open triangle, △), and no in-basin hatchery plus eight dams (open diamond, ◇).



this is the case, then the effect would not accumulate, but rather occur on a year-by-year basis. Unfortunately, we are unable to distinguish among these three possibilities. However, each explanation leads to a distinctly different implication for the status of the wild population involved and selection of the most prudent conservation strategy. In one case, the genetic damage has already been done, in the second the genetic damage may be accumulating, but at such a slow rate it does not yet matter, and finally in the last instance there may be zero lasting damage because the mechanism involved is not genetic, and as soon as the adverse interaction with hatchery fish is removed, the effect will be eliminated.

Our inability to detect a difference between IT and ST hatchery fish in terms of their relative impact on population intrinsic productivity was perplexing. Use of wild fish for hatchery broodstock is a cornerstone of hatchery reforms currently being implemented for salmon and steelhead hatchery programs across much of the Pacific Northwest (USFWS 2010). However, our findings call into question the effectiveness of this path as a means to lessen the impact of hatchery programs on wild populations. The commonly held view is that heavy use of local wild fish in a hatchery broodstock (i.e., IT hatchery programs) will result in hatchery fish that are better adapted to reproduce in the natural environment than hatchery fish from programs where nearly all of the parental stock are of hatchery origin (ISAB 2003; Berejikian and Ford 2004; Araki et al. 2008).

We offer several explanations about why we did not find a difference between populations impacted by ST and IT hatchery fish. First, our finding may be a reflection that the IT hatchery fish in our evaluation were produced by hatchery programs that in many cases did not include enough wild fish in the broodstock to appreciably slow a rapidly progressing domestication process. However, 9 of the 26 populations we classified as containing IT hatchery fish were from situations where 50% to 100% of each year's hatchery broodstock were wild fish. Therefore, in light of this fact, and the reality that for many of the ST hatchery stocks the history of domestication is long and intensive, we conclude that if there were substantive benefits to using IT hatchery fish over ST in terms of natural reproductive performance, we would have detected the signal in our study.

Another possibility for why the impact of hatchery fish from IT programs was indistinguishable of those from ST programs is that the rate at which key genetic traits change for fish in the hatchery environment could be exceedingly rapid. The majority of maladaptive change may occur within one or two generations and be virtually impossible to prevent. Therefore, in terms of reproductive performance in the wild, the genetic damage may occur so quickly that our methods could not detect the short transition period. Instead, what we may have observed was the performance of IT hatchery fish whose reproductive ability in the wild has already been degraded.

Finally, it is possible that the identically adverse effect of IT and ST hatchery fish on recruitment performance may be an indication that the causal mechanism does not have a genetic basis. Perhaps the adverse interaction between large releases of hatchery juveniles and wild juveniles either through competition or perhaps attraction of predators, as suggested by Nickelson (2003), can act to substantially reduce survival and thereby the reproductive performance of a population. Under this explanation, whether or not the hatchery fish in question are genetically similar to the wild population is irrelevant. If this were true, it would be futile to attempt to lessen the adverse impact of hatchery fish on the reproductive performance of a wild population by switching an existing ST hatchery program to an IT hatchery program. IT hatchery programs have some advantages, especially with respect to maintaining genetic lineages; however, from the standpoint of natural recruitment performance it appears that the difference between IT and ST hatchery fish may be inconsequential.

Supplementing natural spawning areas with hatchery fish to benefit the local wild population is a conservation tool that has seen widespread use in the Pacific Northwest (ISAB 2003). The intent of this activity includes re-establishing natural production in vacant habitats, lessening the risk of demographic extinction for wild populations, ensuring the available habitats are seeded to full capacity, and maintenance of genetic lineages. Depending on the circumstances there is a balance between risks and benefits that conservation managers must accurately assess and act on if supplementation programs are to be successful and achieve their intended effect.

It is clear that one of the primary factors that need to be weighed is the degree to which a particular treatment will impact reproductive performance and whether the removal of wild fish from the naturally spawning population to maintain an IT hatchery program is justified. Our results suggest that the net reproductive performance of the population will decline under all hatchery supplementation scenarios. The issue becomes whether the benefits from the supplementation activity, either in terms of reducing extinction risk or maximizing the number of juveniles produced in a basin, is greater than the adverse impacts on per capita recruitment performance. While this question is a topic of research we intend to pursue in the future, we believe there are some general observations that can be offered at this point.

Bringing wild salmonids into a hatchery environment to prevent the extinction of a genetic lineage should only be considered when there is very little likelihood that the population will sustain itself in the wild. Our findings suggest that the productivity of the population will likely be reduced if significant numbers of hatchery reared fish are allowed to spawn naturally, which would further reduce the potential for the population to rebuild. Any re-introduction effort, after the causes for the decline have been addressed, should plan on a period of lower productivity and seek to reduce the number of generations that hatchery fish are allowed to spawn in the wild. Finally, for hatchery programs that are intended primarily to provide fish for fisheries, it appears that integrating wild fish into the hatchery broodstock does not lessen the impact of hatchery fish on the reproductive performance of the wild population. When evaluating or considering such programs, managers should ensure that the benefits to the fishery from an integrated broodstock are clear and unobtainable in other ways, and that the population is productive enough to withstand the impacts from both naturally spawning hatchery fish and the removal of wild spawners.

While using hatchery fish in the short-term to reduce extinction risk and temporarily boost depressed wild populations to re-establish normative biological function are laudable conservation roles, such actions come at a cost in terms of reductions in per capita recruitment performance. Therefore, we conclude, as did Chilcote (2003) and Nickelson (2003), that under most circumstances the long-term conservation of wild populations is best served by the implementation of measures that minimize the interactions between wild and hatchery fish.

Acknowledgements

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Olfactory-mediated stream-finding behavior of migratory adult sea lamprey (*Petromyzon marinus*)

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Abstract: Stream-finding behavior of adult sea lamprey (*Petromyzon marinus*), an anadromous fish that relies on pheromones to locate spawning streams, was documented in the vicinity of an important spawning river in the Great Lakes. Untreated and anosmic migrating sea lampreys were implanted with acoustic transmitters and then released outside the Ocqueoc River. Lampreys swam only at night and then actively. When outside of the river plume, lampreys pursued relatively straight bearings parallel to the shoreline while making frequent vertical excursions. In contrast, when within the plume, lampreys made large turns and exhibited a weak bias towards the river mouth, which one-third of them entered. The behavior of anosmic lampreys resembled that of untreated lampreys outside of the plume, except they pursued a more northerly compass bearing. To locate streams, sea lampreys appear to employ a three-phase odor-mediated strategy that involves an initial search along shorelines while casting vertically, followed by river-water-induced turning that brings them close to the river's mouth, which they then enter using rheotaxis. This novel strategy differs from that of salmonids and appears to offer this poor swimmer adaptive flexibility and suggests ways that pheromonal odors might be used to manage this invasive species.

Résumé : Nous avons étudié le comportement de recherche des cours d'eau chez des grandes lamproies marines (*Petromyzon marinus*) adultes, des poissons anadromes qui utilisent les phéromones pour trouver leurs cours d'eau de fraie, dans les environs d'une importante rivière de reproduction dans les Grands Lacs. Nous avons implanté des émetteurs acoustiques à des grandes lamproies marines migratrices, certaines non traitées et d'autres anosmiques, et les avons libérées à l'extérieur de la rivière Ocqueoc. Les lamproies nagent seulement la nuit, mais de façon active. À l'extérieur du panache de la rivière, les lamproies suivent un cours relativement rectiligne parallèle à la berge, tout en faisant de fréquentes excursions verticales. En revanche, une fois dans le panache, les lamproies font de grands virages et montrent une faible préférence pour l'embouche de la rivière dans laquelle un tiers d'entre elles pénètrent. Le comportement des lamproies anosmiques hors du panache ressemble à celui des lamproies non traitées, excepté qu'elles poursuivent un cap compas plus vers le nord. Pour localiser les cours d'eau, les lamproies semblent utiliser une stratégie en trois phases basée sur les odeurs qui implique une recherche initiale le long de la rive avec des excursions verticales, suivie d'un virage causé par l'eau de la rivière qui les amène près de l'embouchure du cours d'eau, dans lequel elles pénètrent ensuite par rhéotaxie. Cette stratégie inédite diffère de celle des salmonidés et semble fournir une flexibilité adaptative à ce mauvais nageur; elle permet d'imaginer des façons d'utiliser les odeurs des phéromones dans la gestion de cette espèce envahissante.

[Traduit par la Rédaction]

Introduction

Although it is commonly thought that most, if not all, species of anadromous fishes locate spawning rivers from oceans and large lakes using olfactory cues, the orientation mechanisms they use to perform this task are not well understood. Indeed, stream-finding behavior has only been systematically studied in a few species of salmonids, but they all appear to perform vertical excursions while pursuing relatively straight bearings (Quinn et al. 1989; Ogura 1999; Døving and Stabell 2003). After encountering river plumes, salmonids zig-zag through them in a vertical plane in a highly directed fashion while following them more or less directly into river mouths where an odor-based rheotaxis takes over (Johnsen and Hasler 1980; Døving et al. 1985). However, salmonids do not typify all migratory fishes; they are strong swimmers and target specific (natal) streams, discerning odors that they learn as smolts (Hasler and Scholz 1983). In contrast, many species of anadromous fish are not strong swimmers and (or) employ innately recognized odors such as pheromones to locate specific types of streams (Baker and Montgomery 2001; Sorensen et al. 2005). The

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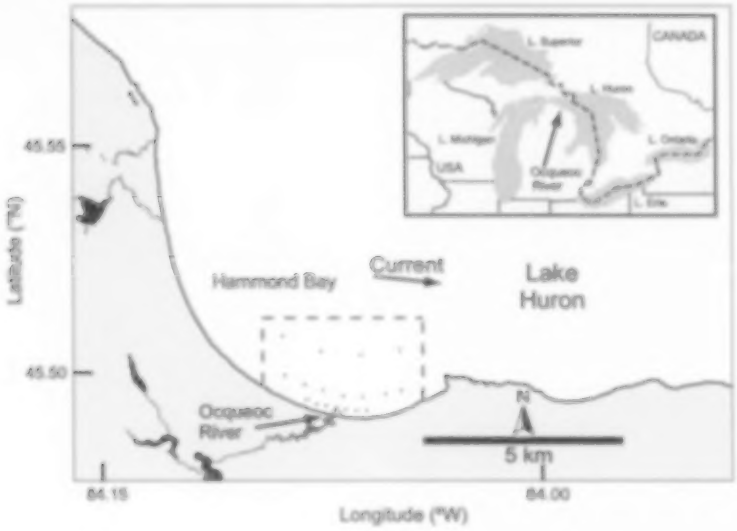
Fig. 1. Research site showing the sampling grid and study area off the mouth of the Ocqueoc River, Michigan. The prevailing direction of the lake current is shown.



latter strategy presumably provides greater flexibility and might be expected to employ different types of orientation mechanisms.

The sea lamprey (*Petromyzon marinus*) is an ancient species of anadromous fish that uses an innately recognized pheromone released by larval conspecifics to locate spawning streams (Sorensen and Hoye 2007). This jawless vertebrate evolved in the Atlantic Ocean several hundred millions of years ago but invaded the upper Great Lakes in the early 20th century where it became landlocked and wreaked great damage because of its parasitic juvenile phase (Bryan et al. 2005; Smith and Tibbles 1980). Sea lampreys spawn and hatch in freshwater streams where they spend several years as filter-feeding larvae before metamorphosing into parasitic juveniles that migrate into the Atlantic Ocean (or large lakes) to feed on other fish. After being carried by far-ranging hosts for approximately 1 year, they cease feeding and seek streams where they spawn and die. Field and laboratory studies of both untreated and olfactory-occluded sea lampreys have clearly demonstrated that these animals recognize streams by odor (Vrieze and Sorensen 2001; Vrieze et al. 2010). Further, these studies have demonstrated that a potent steroidal pheromone released by stream-resident larvae is the key component of stream odor recognized by adults (Sorensen et al. 2005; Fine and Sorensen 2008). This pheromone appears to serve as an innately recognized indicator of quality spawning and nursery habitat because adult sea lampreys show no tendency to return to their home streams (Bergstedt and Seelye 1995) but consistently enter widely scattered Great Lakes streams with large larval populations (Moore and Schleen 1980; Sorensen and Vrieze 2003).

Free-ranging sea lampreys have been shown to be adept at locating streams that have high densities of larval lamprey (Vrieze et al. 2010). Indeed, a recent study found that when sea lampreys were released several kilometres from the Ocqueoc and Cheboygan rivers in Lake Huron, one-third were found in traps of the closest river within 3 days (Vrieze et al. 2010). This study also showed that olfactory cues are a key to this process because when lampreys' olfactory systems were occluded, only one-tenth of these animals found a stream within a several week period. Laboratory studies show similar results (Vrieze and Sorensen 2001). However, how wild, free-ranging sea lampreys locate rivers is not yet known and somewhat puzzling because they are known to be poor swimmers (Beamish 1974, 1979). The present study used acoustic telemetry and river plume measurements in a model river system to address how migratory sea lampreys find spawning streams and their plumes in the Great Lakes. It was hypothesized that migratory adult sea lampreys use different suites of behaviors than homing salmonids. Particular attention was paid to whether sea lampreys search for river plumes using linear swimming and vertical excursions and whether they might locate their source using directed (taxes) or undirected (kineses) behaviors. New insight into the structure of river plumes in lakes, which is poorly understood (Churchill et al. 2003), was also gained.

Materials and methods

Study site and experimental design

This study was conducted in Lake Huron outside the mouth of the Ocqueoc River, Michigan, USA (45.490°N, 84.073°W; Fig. 1), a relatively typical river in the Great Lakes with an average daily discharge of 2.8 $m \cdot s^{-1}$. At the time of the study (2001–2002), the Ocqueoc River contained a large population of larval lampreys (Klar and Young 2003), and its water had been shown to both contain the key components of the larval pheromone (Fine and Sorensen 2005) and to attract adult sea lampreys in the laboratory (Vrieze and Sorensen 2001). Three experiments were conducted, the first of which determined whether sea lampreys exhibit daily activity cycles so that subsequent efforts could focus on periods of maximum activity. The second exam-

ined the movement patterns of sea lampreys swimming within the river plume and outside of the river plume. A third experiment examined the movement patterns of sea lampreys that had been rendered anosmic. These are described following a brief description of the experimental animals.

Experimental animals

Sea lampreys were captured in riverine traps (box traps and fyke nets) as they migrated into the Ocqueoc River and other nearby rivers and then transported to Hammond Bay Biological Station (Millersburg, Michigan, USA) where they were held in flowing Lake Huron water until needed. Previous studies have shown that the capture and transport procedures used do not affect sea lamprey behavior and that the site of capture does not influence lamprey behavior (Vrieze et al. 2010). Large, healthy, nonovulated maturing females (535 ± 30 mm in total length (TL), 321 ± 48 g) were selected for these studies because their larger body cavities and mass of soft, ovarian tissue (up to 25% of fish biomass) easily accommodated acoustic transmitters, and previous studies have shown that behavior of maturing females is no different than that of maturing males (Bjerselius et al. 2000). Lampreys were anaesthetized (0.02% clove oil; Munday and Wilson 1997), a 1.5 cm incision made in their coelomic cavities, and either a non-depth-sensing transmitter (Lotek Wireless Inc., Newmarket, Ontario, Canada; CAFT8_6; 4.2 g) or a larger, depth-sensing transmitter (CTP-A11-12; 8.3 g; precision of 0.6 m) was inserted. Transmitters were sterilized in alcohol prior to insertion. The incision was closed with a suture (monofilament nylon Ethilon 3-0 FS-1, Ethicon Inc., New Brunswick, New Jersey, USA), a plastic anchor tag (Avery Dennision Inc., Pasadena, California, USA) inserted into the dorsal musculature, and the fish was revived in lake water. Generally, sea lampreys were released within a few days of treatment. Pilot laboratory studies in which sea lampreys were exercised in a swim tube showed no effect of tagging on either the health or swimming performance of sea lampreys (n = 8; see Vrieze 2008). Post hoc analyses of wild sea lamprey movement also showed that lamprey swimming speed was not influenced by transmitter size (n = 32; p = 0.91). Range testing of these tags and evaluation of their technical specifications showed that they were consistently detected at distances greater than 0.5 km and that their performance was seemingly not altered by the temperatures and conductivities lampreys encountered (L. Vrieze, unpublished data; Lotek Wereless Inc., Newmarket, Ontario, Canada, personal communication).

Sea lampreys were released and tracked whenever the weather permitted in April–July 2001 and 2002 (their migratory–spawning season). Each day that lampreys were released, the distribution of the Ocqueoc River plume was mapped across a 2 km × 4 km, 21-position sampling grid in front of its mouth ("study area"; Fig. 1). This was accomplished by measuring water conductivity throughout the water column to a depth of 25 m using a sonde (MiniSonde Multiprobe, Hydrolab Corporation, Loveland, Colorado, USA) and took advantage of the fact that river water conductivity was typically at least 40 microsiemans (μS) greater than that of water from the open lake. River water concentrations were calculated using linear regression, with 100% river water being the conductivity of water measured in the river's mouth, and 0% being the lowest value recorded within the sampling grid that day. Inverse distance weighting was used to interpolate unsampled areas (Watson 1992). Post hoc plots of the variation in lake and river water conductivity showed that 10% dilutions of river water could be reliably measured (Vrieze 2008).

Implanted sea lampreys were released by transporting them to their release site in coolers and carefully emptying them over the side of a boat. After approximately 15 min, lampreys were located using a unidirectional hydrophone with receiver, which decoded acoustic signals (Lotek SRX400, Newmarket, Ontario, Canada). Lamprey position was determined by maneuvering the boat around a central point until signal strength was gauged to be equivalent from all points of the compass, indicating the animal was underneath the boat. These positions were later used to plot lamprey tracks. If appropriate, animal depth information was also collected. Water conductivity and temperature were also measured at the surface and several depths to either the bottom or a depth of 25 m. Post hoc analyses of the positions of lampreys thought to be stationary (experiment 1) showed that on average we located lamprey positions with a precision of approximately 16 m (N = 102 measurements of 17 lampreys). All procedures were approved by the University of Minnesota Institutional Animal Use and Care Committee.

Experiment 1: determining daily activity

Our first experiment sought to determine whether lacustrine sea lampreys exhibit daily patterns of activity so that subsequent experiments could focus on appropriate times of the day. In June 2001, we released sea lampreys in groups of 3 or 4 at 0400 (n = 6), 1200 (n = 10), and 2000 (n = 9) into the center of our study area. Individual lampreys were then located and monitored for ~30 min intervals to determine if they were either moving (their positions appeared to change by more than 50 m) or not, before locating and monitoring another lamprey. We rotated through all members of each group that remained within the study area for 12–14 h (excluding a 3 h crew change midway through the experiment). If lampreys from previous groups were re-encountered, their activity was monitored also. For analysis, we determined the percentage of the located lampreys that were moving in each hour. Initial analysis suggested that lamprey tendency to move was not influenced by the presence of river water (p > 0.10), so data collected inside and outside of the river plume were combined and plotted together.

Experiment 2: determining sea lamprey movement patterns inside and outside of the river plume

This experiment took place in June–July of 2001 and April–June 2002 and focused on describing sea lamprey activity both within and outside of the river plume and its associated odor. Individual implanted lampreys (n = 26) were released each night between 2100 and 0100 and relocated approximately every 15 min for 3–6 h. If lampreys did not appear to move more than 50 m for 90 min after release, they were considered to not be moving and abandoned (n = 3). Release sites alternated between locations inside and out-

side of the plume, with the majority of the lampreys carrying depth-sensitive transmitters.

Experiment 3: determining the role of olfaction in sea lamprey movement patterns

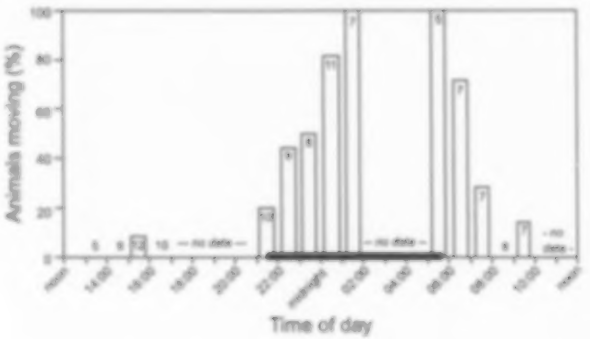
To determine the role of olfactory cues in sea lamprey search behavior, six lampreys were rendered anosmic by injecting dental impression material (3M Express vinyl polysiloxane, St. Paul, Minnesota, USA) into their nasopores during tag implantation (see Vrieze et al. 2010 for details). Animals were released outside the plume because these locations had deeper water and we wanted to collect detailed information on depth distribution. This method of olfactory occlusion is known not to affect animal health or swimming performance (Vrieze and Sorensen 2001; Vrieze et al. 2010). Animals were tracked as described for experiment 2.

Tracking analysis of experiments 2 and 3

For analysis, the entire path swam by each lamprey was defined as its "track", while the distances between individual lamprey positions along that path were defined as "segments". We plotted all tracks and then examined segments within them to characterize each animal's gross movement patterns. The bearings of each track segment to both magnetic north (compass bearing; North = 0°) and the river mouth (river heading; movement towards the river mouth = 0°) were calculated. Trends in track compass bearings were then evaluated using first-order Rayleigh tests on its segments (Batschelet 1981), while trends in river headings were tested versus 90° using one-sample t tests (Statistica, StatSoft Inc., Tulsa, Oklahoma, USA; significance evaluated at $p < 0.05$). Turning angles were calculated by measuring the angles between segments (0°–180°), and the distribution of all of these angles was evaluated after placing into 30° bins. Ground speed was calculated for each segment and averaged across each track for lampreys deemed to be swimming. To evaluate the linearity of each track (track linearity), the sum of all its segments was divided by the direct distance between the track's first and last positions (e.g., 1.0 = a perfect line). The tendency of individual lampreys to move towards or away from shore was evaluated by calculating the sum of the distances each lamprey swam either toward or away from the shoreline for each segment and then dividing this by the sum of all segments to produce a "shore index" (e.g., 1 = towards shore; –1 = away from shore). Shore indices for each track were tested against 0.0 (no bias) using one-sample t tests (Statistica; significance evaluated at $p < 0.05$). To describe the tendency of individual lampreys to make vertical excursions (dive), we calculated the number of times each animal changed its depth by more than 10 m in each segment and divided this by the total time that depth measurements were made in water deeper than 10 m. Finally, the tendency of lampreys to swim near the surface was evaluated by calculating time spent within 0.6 m bins within the top 3 m and plotted.

Once track information had been characterized, differences between tracks of lampreys in each treatment group were evaluated. The effects of the river plume on lamprey swimming were evaluated by comparing the behavior of animals outside the plume with those released inside using paired t tests after testing for normality. Depth analyses used Mann–Whitney U tests because these values were not normally distributed. Biases in the compass bearings of treatment groups were evaluated using second-order Rayleigh tests, which produce a statistic r whose value ranges from 0.0 for random movement to 1.0 for perfectly uniform movement patterns (Batschelet 1981). The turning angles of untreated sea lampreys located outside and inside of the plume were then compared by calculating the average distribution of the turning angles of their respective tracks and comparing these values by χ^2. Finally, differences between anomsic and untreated lampreys released outside of the plume were compared using t tests (Statistica). Standard deviations were calculated as an index of variability within each group. Directional concentration (r) was used as the index of variability for compass bearing (Batschelet 1981).

Fig. 2. The relative number of active (swimming) sea lamprey at different times of the day (experiment 1). The numbers inside the bars denote the number of individuals located at each time period. The black bar on the x axis indicates scotophase (nighttime). Unless noted otherwise, the absence of a bar means that no lampreys were moving.



Results

Sea lamprey swimming activity was strongly nocturnal, with activity peaking after midnight (Fig. 2). At both 0100 and 0500, all lampreys were moving and this number dropped to ~60% at daybreak (0600) and then decreased to 0%–10% by 1000. Lampreys were rarely observed moving at midday (1 of 12 animals between 1500 and 1600). On two occasions during the day, lampreys were observed motionless on the bottom, and on other occasions they appeared to be in or under piles of rocks.

In experiment 2, nearly all sea lampreys released outside of the plume swam actively (11 of 14) and then at a relatively fast speed (average ground speed was 1.5 km·h^{-1}; average maximum of 2.1 km·h^{-1}; Table 1; Fig. 3). Movement rate was bimodally distributed; 8 of 11 lampreys swam quickly and had average ground speeds of 1.9 km·h^{-1}, while three traveled at a rate of less than 0.5 km·h^{-1}. Lampreys swam continuously and consistently in a highly linear manner while making only an occasional small-angle turn and performing frequent and extensive vertical excursions (approximately every third minute, often to the bottom) (Table 1; Fig. 3). Most tracks (8 of 11) had a compass bias ($p < 0.05$) to the northwest and only one had a significant shoreward bias (Table 1; Fig. 4). Nevertheless,

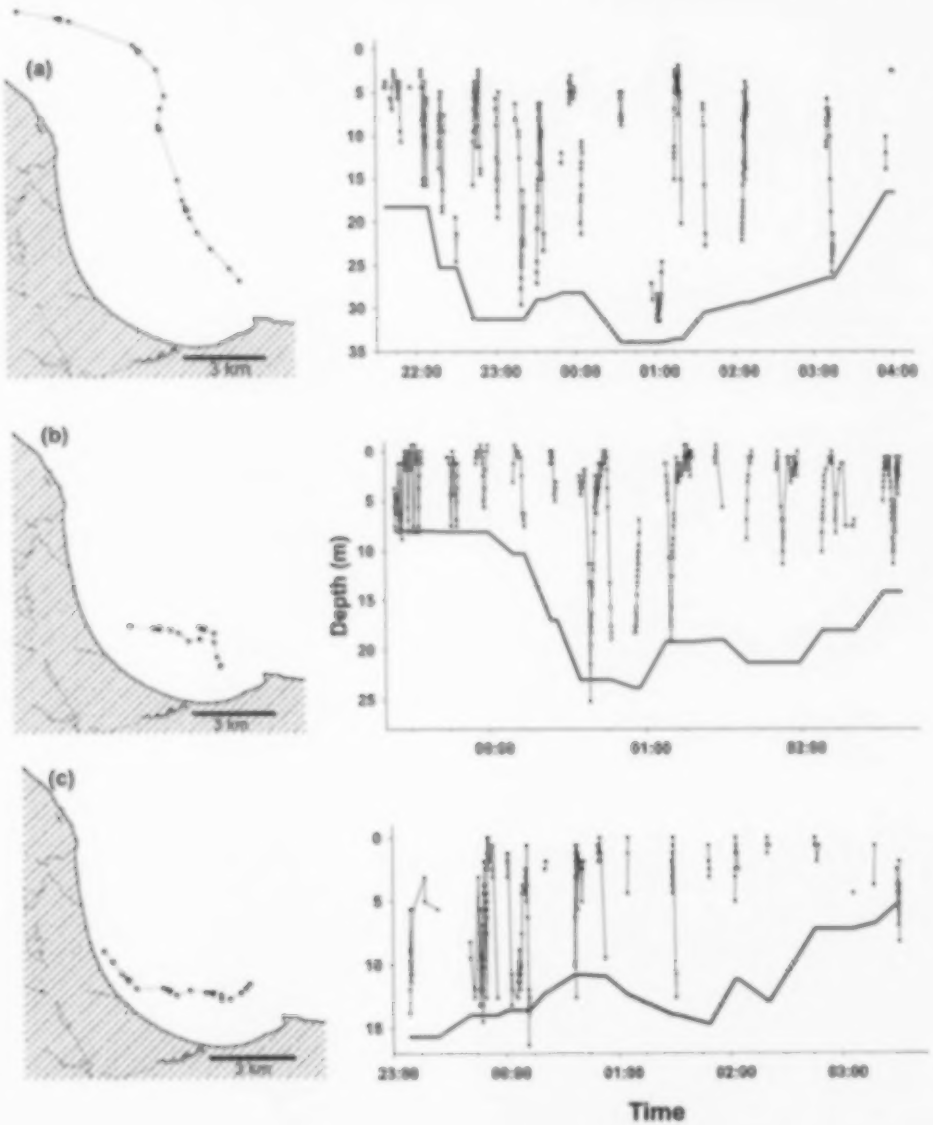
Table 1. Characteristics of sea lamprey swimming behavior observed outside the Ocqueoc River plume, within the plume, and after olfactory-occlusion.

Treatment	*n*	Ground speed ($km \cdot h^{-1}$)	Track linearity	Turning angle	Compass bearing	River heading	Shore index	Vertical excursions ($no. \cdot min^{-1}$)
Outside plume	11	1.5 (0.9)	0.76 (0.12)	38° (18)	311° (0.30)	115° (38)	0.09 (0.26)	0.35 (0.28)
Inside plume	11	1.2 (0.4)	0.44 (0.26)*	58° (18)*	251° (0.32)*	52° (28)*	0.10 (0.17)	0.23 (0.25)
Anosmic	5	1.1 (0.6)	0.70 (0.17)	41° (33)	343° (0.62)	120° (37)	–0.52 (0.25)*	0.30 (0.17)

Note: Means value of the tracks for each treatment is shown along with standard deviation (in parentheses), with the *r* statistic being shown for compass bearing.

*Different than animals outside of the plume ($p < 0.05$; see text for exact values).

Fig. 3. Movement patterns of three representative sea lampreys released outside of the river plume (experiment 2). The figures on the left show the horizontal movements of individual lampreys within Hammond Bay, while the figures immediately to the right show the corresponding positions of the same lampreys with respect to depth (*y* axis) and time (*x* axis) for each track. The position of the bottom of the lake is noted.



as a group, compass bearing was not in a consistent direction ($p = 0.29$) (Table 1). Sea lampreys rarely came within the top 0.6 m of the surface, and no lamprey released outside of the plume entered it.

All 12 of the sea lampreys released inside of the river plume moved at a rate comparable to that of lampreys released outside of the plume ($p = 0.46$; Table 1), although the manner with which they swam was very different. In particular, lampreys inside of the plume swam in large circles (Fig. 5), which gave them a bias towards the river mouth (heading; $p = 0.0013$) and which four lampreys entered directly. Three lampreys were tracked in the river for 30 min and did not leave (Fig. 5*c*). Both track linearity ($p = 0.0013$) and the distribution of turning angles ($\chi^2 = 14.2$; df = 4) differed between lampreys located inside and outside of the plume, with almost a quarter of all turns inside the plume being greater than 90°, while animals outside the plume very rarely turned more than 90° (Fig. 6). However, similar to lampreys located outside of the plume, lampreys inside the plume performed frequent equivalent numbers of dives ($p = 0.45$; Table 1), which often brought them to lake bottom. Tracks of individuals located in the plume tended to show a weak compass directionality (3 of 12 tracks were significant at $p < 0.05$), while the group as a whole had a strong bias to the southwest (Fig. 4; second-order Rayleigh test for the group was significant at $p = 0.005$). Lampreys released within the plume tended to favor the upper 0.6 m of the water column compared with animals located outside of the plume ($\chi^2 = 6.6$; $p = 0.01$; Fig. 7).

Five of the six anosmic sea lampreys swam actively with an average ground speed equivalent to that of untreated animals (1.1 km·h^{-1}; Table 1; $p = 0.48$), with an average maximum of 1.7 km·h^{-1}. All anosmic lampreys swam in a highly linear fashion while actively performing vertical excursion at rates that did not differ from untreated lampreys outside of the plume ($p = 0.61$; Table 1; Fig. 8). These animals swam with a more northerly compass bearing (three of which were significant; $p < 0.05$) than did untreated animals, which took them offshore and gave them a different overall shore bearing ($p = 0.0006$). The tracks of these animals were notably invariant (Table 1). None entered either the plume or the river.

In addition to describing sea lamprey movement, this study documented dramatic daily and seasonal changes in the Ocqueoc River plume. The structure of the plume changed with the season, while its extent and directionality fluctuated on a daily basis. Just after ice-out in early April 2002, the river water temperatures were colder than the lake, and the plume was submerged. However, within a week it had warmed enough to become superficial where it remained for the rest of the season becoming increasingly thin with time. By July the plume was restricted to the top 0.6 m of the lake (i.e., many lampreys swam under it), although it thickened during times of high wind and river flow. Daily fluctuations in plume extent were commonplace. In the late spring when river flows were high, it often extended over 3.5 km from the river mouth, but by midsummer it was often only 0.5 km from the river mouth. Typically, the plume flowed to the north in a tongue-like fashion, but occasional wind shifts caused it to move to the west and accumulate in the immediate vicinity of that shore-

Fig. 4. Mean compass bearings of sea lampreys released: (*a*) outside the river plume or (*b*) inside the plume. Panel (*c*) shows anosmic animals released outside the plume. Each arrow represents the mean bearing of a single animal to north (0), while the crosshairs represent the second-order mean angle of the group. The length of the arrows indicates the overall strength of directional concentration (*r*; 0 = random directional distribution; 1.0 = uniform directional distribution).

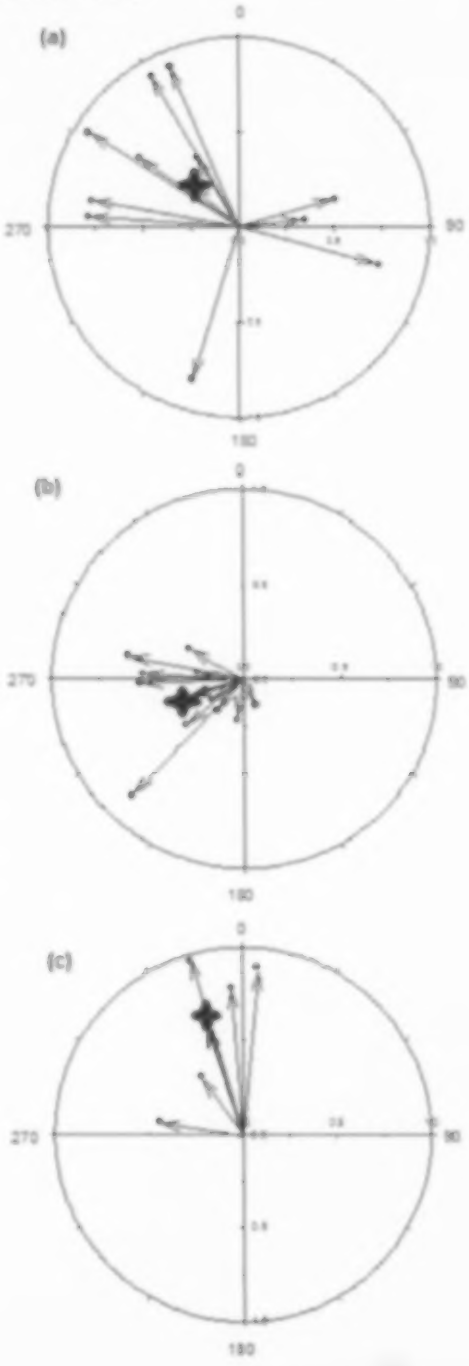
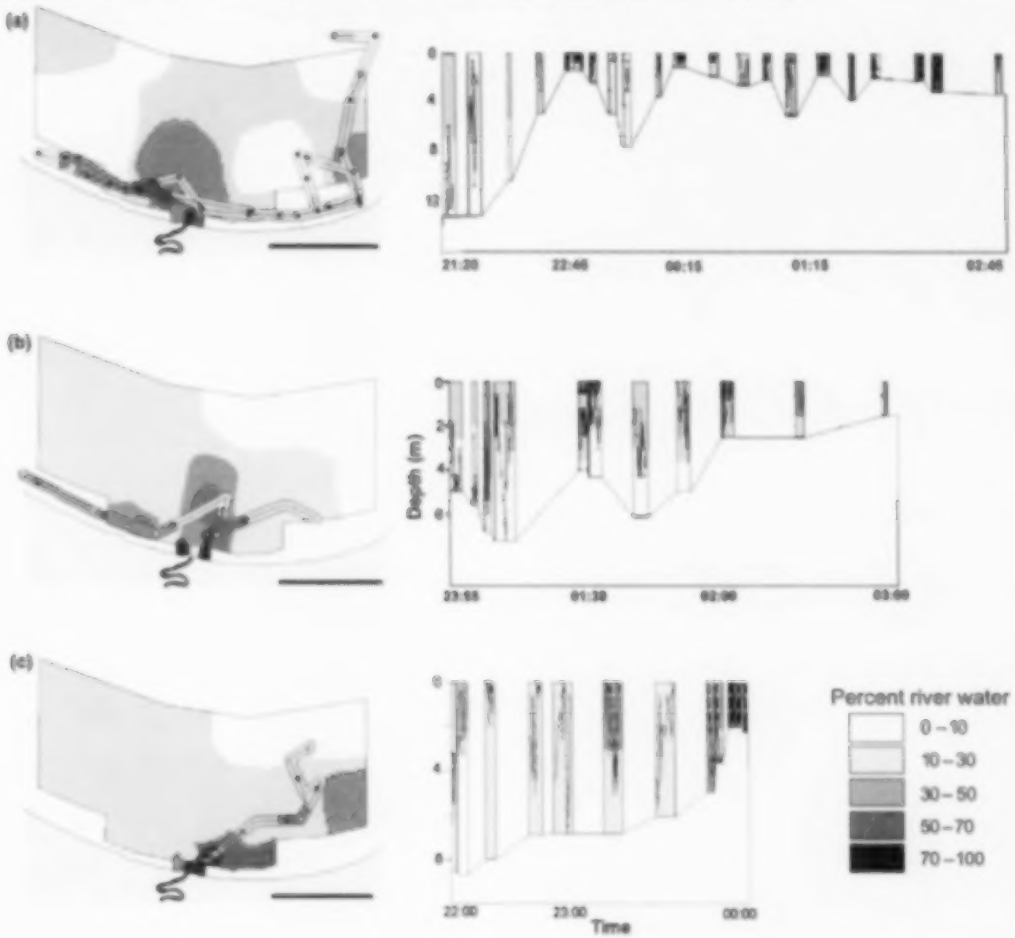


Fig. 5. Movement patterns of three representative sea lampreys released inside of the Ocqueoc River plume and the concentration of river water (experiment 2). The figures on the left show the horizontal movements of individual lampreys within Hammond Bay, while the figures on the right show the corresponding positions of the same lampreys with respect to depth (*y* axis) and time (*x* axis) for each track. The lamprey in panel (*c*) entered the river and did not leave. River water concentrations were measured across the grid prior to lamprey release and are shown in the background as five different levels of shading. River water measurements taken during tracking are superimposed on top of the background (small shifts in river plume often occurred during the day). Scale bars are 1 km.



line. Lake current in the vicinity of the plume was measured on several occasions and was found to be flowing to the east at approximately 0.5 km·h^{-1}.

Discussion

Migratory adult sea lampreys seeking spawning streams exhibited a remarkable set of complex, active, and novel behaviors that could be divided into three phases: search, approach, and river entry. The basic sequence of these behaviors was similar to that described for migratory Pacific salmon (*Oncorhynchus* spp.) and Atlantic salmon (*Salmo salar*) seeking a natal stream, although key aspects are fundamentally different and reflect different solutions to related problems. In all of these species, the initial search for an odorous river plume in open waters appears to be characterized by extremely vigorous linear swimming while casting (diving) vertically to considerable depths. However, unlike salmonids, sea lampreys were inactive during the day. Similarly, once within a plume, both salmonids and sea lamprey adopt approach behaviors characterized by changes in turning behavior, although for salmonids this is associated with changes in diving behavior and a directed movement towards the odor source, while lampreys appeared to turn in the horizontal plane in an undirected manner that increased their chances of remaining within the plume. Finally, although we collected few details on how lampreys entered the river mouth, it appeared to reflect a rapid directed movement, perhaps akin to the odor-mediated rheotaxis exhibited by Pacific salmon (Johnsen 1982). Together, this suite of behaviors appears to guide lampreys to rivers with good spawning habitat without restricting this relatively poor swimmer to specific rivers.

Fig. 6. Turning behaviors of sea lampreys located outside (open bars) and inside (solid bars) of the river plume. Turning angles were binned by 30-degree increments. Medians and quartiles are shown.

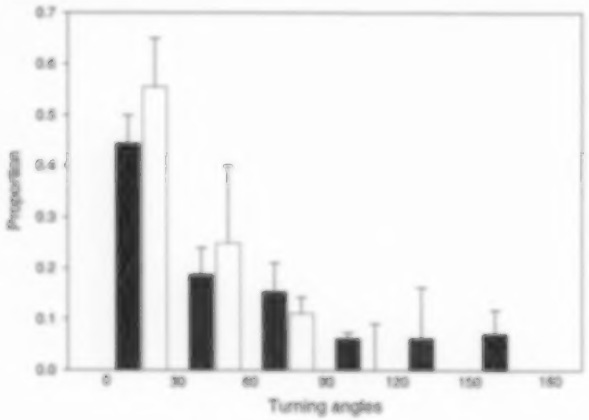
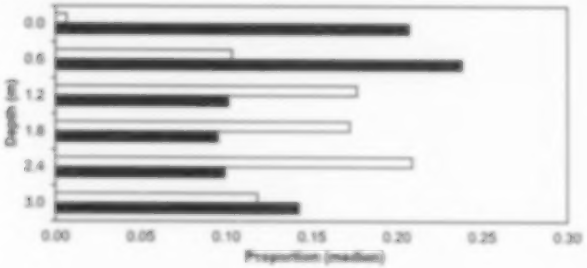


Fig. 7. Relative time (median) spent by sea lampreys at different depths within 3 m of the surface (solid bars = animals within the plume; open bars = animals outside of the plume; $p < 0.05$ for 0–0.6 m bin).



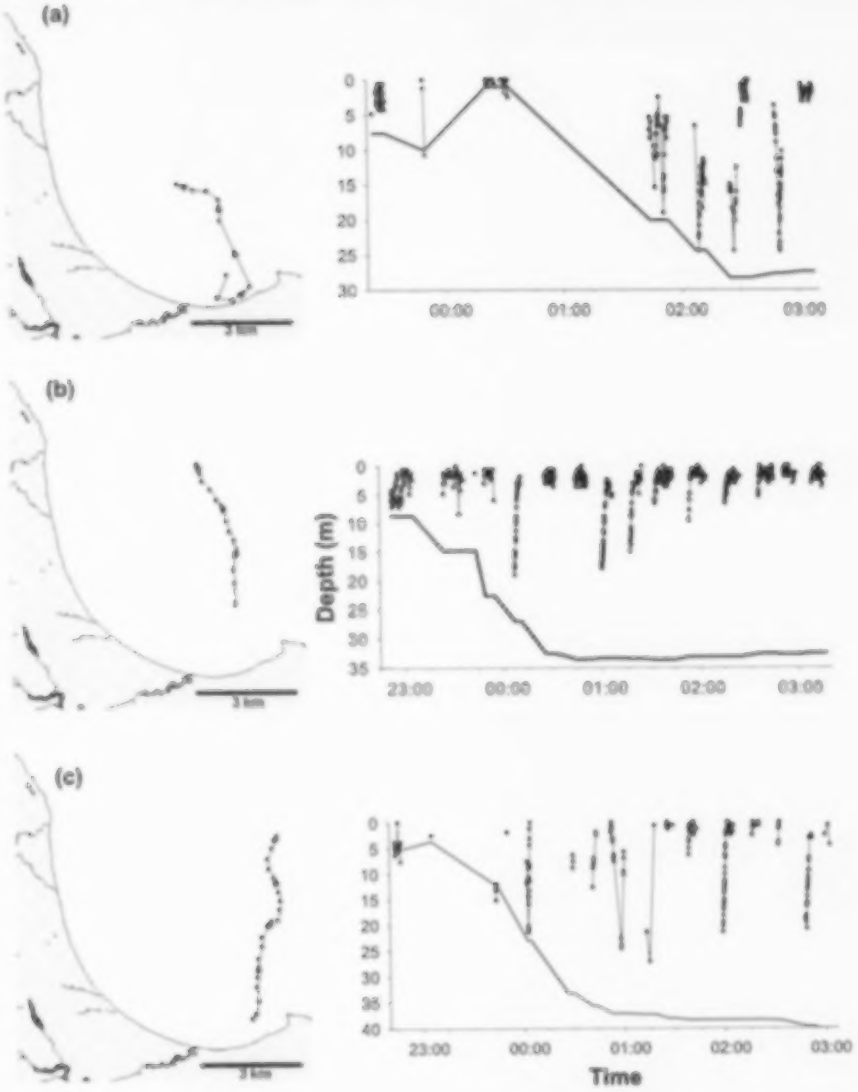
The linear search behavior exhibited by sea lampreys outside of the river plume appeared very similar to that of many other organisms, including salmonids and some insects, and appears to reflect an efficient strategy to find an object in the absence of information (Jander 1975; Dusenbery 1992; Bell et al. 1995). Although many species of migratory fish in addition to Pacific salmon appear to search in this manner (Quinn et al. 1989; Brill et al. 1993, 2002), several facets of the lamprey's search were notable. First, the rate at which lacustrine sea lampreys swam (estimated ground speed was ~1 body length·s^{-1}) exceeded that previously measured in the laboratory, even without considering the *z* axis (Beamish 1974, 1979). Second, their activity pattern was strongly nocturnal. This pattern may allow them to rest from predators and appears to persist once they have entered streams (Almeida et al. 2002). Third, they swam surprisingly straight tracks while paralleling shore. It is also possible that this behavior reflected a lateral-line-driven response to lake current (Ayali et al. 2009); certainly, it assisted in plume finding. Fourth, lampreys repeatedly and extensively dove throughout the water column. Vertical casting is commonly used by teleost fishes and is an efficient way to search for layered, odorous river waters (DeBose and Nevitt 2008). This multifaceted search strategy has presumably served the sea lamprey well in its search for suitable spawning streams across its broad and diverse geographic range.

In contrast with the linear swimming exhibited by lampreys outside of the Ocqueoc River plume, lampreys released within the plume turned frequently and in large circles. This circling behavior, which some authors might consider a component of an approach or "close-search" strategy (Dusenbery 1992), imparted a weak but consistent bias towards the river mouth, which a third of the lampreys eventually entered. Similar behaviors are seen in flying insects, which often circle ever more tightly as they approach their goal and stimulus strength increases (Dusenbery 1992). In the case of the sea lamprey, this circling behavior appeared to reflect a simple klinokenesis (Frankael and Gunn 1961), or undirected change in turning rates, because the lampreys did not appear to turn more sharply in higher concentration river water and many animals swam right past the river mouth. Stream studies also suggest that lampreys are not adept at tracking odor concentration gradients (Wagner et al. 2009). Free-ranging lampreys also spent more time in surface waters when in the plume, suggesting that exposure to odor may alter diving behavior (casting) in an adaptive fashion. Notably, sea lamprey swimming speed did not change in river water as would be expected if this behavior was an orthokenesis (Perez 1969). The fact that a third of lampreys entered the river (a value similar to that observed by Vrieze et al. 2010) suggests that this strategy is reasonably effective. It is possible, but unknown, whether lampreys that missed the Ocqueoc River entered other streams.

Although little data were collected on river entry, once in the river mouth lampreys appeared to enter directly, suggesting that this response might reflect an odor-driven rheotaxis or movement into current flow (Dusenbery 1992; DeBose and Nevitt 2008). Similar responses have been observed in Pacific salmon and can be very effective (Johnsen 1982). We and others have noted a strong tendency of riverine lampreys to swim upstream (Stier and Kynard 1986; Almeida et al. 2002; Vrieze et al. 2010). Sex pheromonal odors appear to eventually direct final upstream movement in fully mature sea lampreys (Johnson et al. 2009).

When taken as whole, and in the context of previous studies on lamprey olfactory biology, the results of this study support the possibility that stream finding is primarily driven by stream odor and the larval pheromone in particular. The swimming behavior of olfactory occluded lampreys was virtually identical to that of osmic lampreys located outside of the plume where no odor was found. Indeed, the only difference was a small but consistent difference in compass bearing. It is possible that this might have reflected a role for magneto-electrosensitivity (Chun-Davidson et al. 2008) in the complete absence of odor. Notably, laboratory studies have also shown that stream water localization in sea lampreys is entirely dependent upon a functional olfactory system, that Ocqueoc River water is detected even when diluted over 100-fold, and that lampreys immersed in it exhibit extensive turning behavior but no change in speed (Vrieze and Sorensen 2001). Finally, large-scale mark–recapture studies in several river systems have also shown that the sea lamprey relies on olfactory cues to find these

Fig. 8. Movement patterns of three representative anosmic sea lampreys released outside of the river plume (experiment 3). Panels at the left show horizontal movement, while the panels on the right show depth and time for each sea lamprey. No river water was detected. The scale bars are 3 km.



systems (Vrieze et al. 2010). Future studies should nevertheless attempt to examine the role of olfaction within the plume to confirm the specifics of this behavior, especially if means are developed to track plume odor with greater precision.

The complex but flexible stream-finding behavior of the sea lamprey is likely of high adaptive importance to this ancient species of fish. If the variation we observed in the Ocqueoc River plume is typical, sea lampreys must cope with an enormous variety of river plumes across their geographic range, which includes both sides of the Atlantic Ocean and the Laurentian Great Lakes. Their apparent tendency to search by following shorelines should give them a good chance of finding a stream no matter where and when parasitic phase juvenile lampreys leave their hosts. Similarly, vertical casting behavior, coupled with the extraordinary sensitivity of their olfactory system (10^{-13} mol·L^{-1} detection threshold; Fine and Sorensen 2008), should allow them to locate river plumes at almost any depth or location. Their dependence upon a pheromone is also adaptive because it can serve as a reliable indicator of spawning habitat quality, allowing them to find streams with the most discernable plumes, not necessarily the first one encountered. Because the pheromone has been synthesized (Hoye et al. 2007), our understanding of search and localization strategies could help guide sea lamprey control in the Great Lakes and restoration of other lamprey species elsewhere that appear to use similar behaviors and pheromonal cues (Robinson et al.

2009). Pheromone application for lamprey management should probably choose streams with strong and persistent plumes and need only be performed at night. Stream localization mechanisms used by stronger swimming, anadromous teleost fish seeking pheromones would similarly be interesting to evaluate.

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Maternal and paternal effects on fitness correlates in outbred and inbred Atlantic salmon (*Salmo salar*)

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Abstract: Small populations are at risk of fitness reductions due to inbreeding depression and the loss of within-population genetic diversity. Although this risk can be mitigated by interpopulation outbreeding, any increases in genetic variability may be offset by reductions in fitness attributable to outbreeding depression. Here, we evaluate the risks of inbreeding and outbreeding by quantifying changes in survival and seven other fitness-related traits expressed in early life (e.g., specific growth rate, development time), using three small and neighbouring populations of Atlantic salmon (*Salmo salar*) reared under a common-garden experimental protocol. After accounting for parental (maternal and paternal) effects on several traits (which differed between pure and F_1 outbred parents), we detected no significant cross type-level differences between inbred and pure (non-inbred, within-population) cross types, outbred and pure cross types, or inbred and outbred cross types. The extent to which parental effects on fitness-related traits might be considered beneficial or detrimental cannot be reliably determined in the absence of information on the adaptive significance of the trait values in the local environment.

Résumé : Les petites populations risquent une réduction de leur fitness à cause de la dépression consanguine et de la perte de diversité génétique à l'intérieur de la population. Bien que ce risque puisse être mitigé par des croisements exogames entre les populations, toute augmentation de la variabilité génétique peut être neutralisée par des réductions de la fitness attribuables à la dépression exogame. Nous évaluons ici les risques de l'endogamie et de l'exogamie en mesurant les changements dans la survie et dans sept autres traits reliés à la fitness qui se manifestent dans les premiers stades de vie (par ex., le taux de croissance spécifique, la durée du développement) chez trois petites populations avoisinantes de saumons atlantiques (*Salmo salar*) élevées selon un protocole expérimental de jardin commun. Après avoir tenu compte des effets parentaux (maternels et paternels) sur plusieurs traits (qui diffèrent entre les parents purs et exogames de F_1), nous ne décelons aucune différence en fonction des modes de croisement, entre les types de croisement endogames et purs (sans endogamie, au sein même de la population), entre les types de croisement exogames et purs, ni entre les types de croisement endogames et exogames. Il n'est pas possible de déterminer avec assurance dans quelle mesure les effets parentaux sur les traits reliés à la fitness peuvent être avantageux ou nuisibles sans avoir de renseignements sur l'importance adaptative de la valeur de ces traits dans l'environnement local.

[Traduit par la Rédaction]

Introduction

Many species are increasingly composed of small, isolated populations because of widespread, human-induced habitat change and loss (Frankham 2005). Such species may have an elevated risk of extinction because of a variety of threats, including those of a genetic nature. For example, small population size often results in disproportionately faster rates by which genetic diversity is lost via genetic drift (Frankel 1974; Frankham 2005). Inbreeding at low abundance can also reduce individual fitness because of the expression of recessive deleterious alleles (i.e., inbreeding depression: Charlesworth and Charlesworth 1987; Saccheri et al. 1998; Crnokrak and Roff 1999). In turn, either factor may reduce the capacity of populations to adapt to environmental change or further hinder population recovery after other demographic threats, such as habitat alteration, have been removed (Frankham et al. 2002; Spielman et al. 2004).

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To some extent, these genetic threats can be mitigated with well-planned supportive or captive breeding programs (cf., Frankham 2008; Fraser 2008). Alternatively, there may be some merit to interbreeding small but genetically related populations, especially once captive breeding has become essential to avoid extirpation in the wild. Interbreeding may produce outbred offspring with higher fitness because the offspring contain new beneficial alleles and have increased locus heterozygosity (i.e., heterosis, Emlen 1991; Whitlock et al. 2000; Vergeer et al. 2004). Similarly, interbreeding has the potential to generate greater genetic variability in outbred individuals, which may increase the ability of a population to persist in stochastically variable environments and may ultimately contribute positively to population growth (i.e., "genetic rescue"; Tallmon et al. 2004).

Nevertheless, intentional interbreeding of even apparently closely-related populations is not without risks. Outbred individuals generated may, alternatively, have reduced fitness relative to pure parents, owing to outbreeding depression, either through the loss of local adaptation (extrinsic outbreeding depression) or the disruption of co-adapted gene complexes (intrinsic outbreeding depression) (Dobzhansky 1950; Templeton 1986). Furthermore, although a few empirical studies have shown that the severity of outbreeding depression can be positively related to genetic differentiation at neutral genetic markers (Edmands 1999; 2002; but see McClelland and Naish 2007), theoretical work suggests that interbreeding between populations of small genetic differentiation may generate variable effects (Edmands and Timmerman 2003). In fact, Lynch (2000) suggests that the interaction of genomes from populations may not be predictable because the processes of fixation and mutation are random among populations.

The question of whether or not to interbreed populations is thus an important, understudied, and contentious issue in conservation biology (Edmands 2007). This may be especially true for a growing number of species rehabilitation projects involving declining populations of salmonid fishes (Fraser 2008). Indeed, salmonids exhibit a high degree of population diversity in phenotypic traits, putative local adaptations, and population genetic differentiation even at fine geographic scales, with the latter having been routinely screened at neutral genetic markers and applied in management contexts for 40 years (Utter 2004; Fraser 2008, references therein). Nonetheless, it is largely unknown whether population genetic data are useful as indicators of quantitative trait diversity, inbreeding depression, or outbred fitness in salmonids (Mavarez et al. 2009). In part, this is because few studies have examined the fitness outcomes of crossing multiple populations (Gilk et al. 2004; McClelland and Naish 2007; Fraser et al. 2010). We are unaware of any empirical study on a salmonid that has examined potential trade-offs between inbreeding and outbreeding depression concurrently.

Wild Atlantic salmon (*Salmo salar*) populations worldwide have suffered extirpations and large declines in population size (WWF 2001). Live Gene Banking (captive breeding) efforts of endangered Inner Bay of Fundy (IBoF) populations in eastern Canada have resulted in an increase in the number of juveniles in rivers that receive support, but this increase is not projected to result in the recovery of IBoF populations while salmon mortality at sea remains unusually high (DFO 2008). There are concerns that inbreeding and reduced within-population genetic diversity may also be impeding the recovery of IBoF Atlantic salmon (DFO 2008). There are also concerns that the use of outbreeding to mitigate genetic threats associated with inbreeding and genetic drift in small, fragmented populations — even between neighbouring populations — may result in outbreeding depression, given the literature on inter-population outbreeding in salmonids (e.g., Gharrett et al. 1999; McGinnity et al. 2003; Fraser et al. 2008).

Our objective was, thus, to evaluate the relative fitness of inbred and interpopulation outbred cross types, using three small and declining neighbouring Atlantic salmon populations of the IBoF. Fitness-related traits were measured during the early-life history stages in a common-garden laboratory environment. Observations were taken on survival and several salmonid fitness-related traits (e.g., egg diameter and development time to 50% hatch). In light of the foregoing theoretical and empirically-based concerns, we suggest there may be considerable merit in comparing the relative fitness of inbred and outbred cross types, using neighbouring populations, as a basis for providing advice to those managing the recovery of endangered Atlantic salmon in eastern Canada and of populations of species at heightened extinction risk elsewhere.

Materials and methods

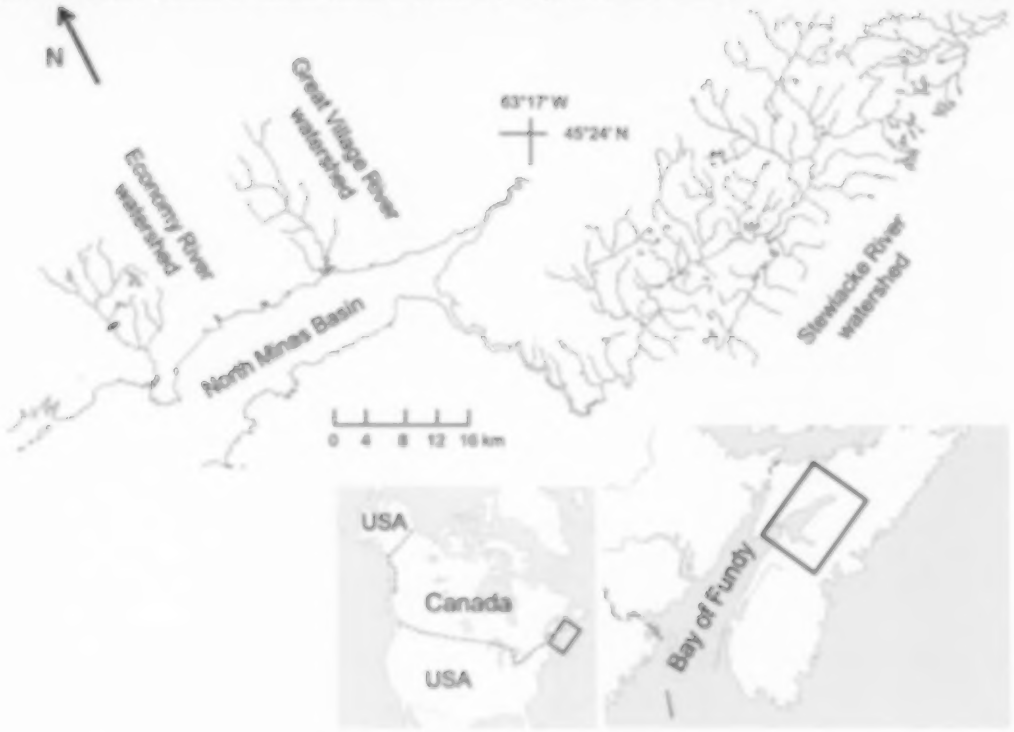
Study populations

Three Nova Scotian populations of Atlantic salmon from the Inner Bay of Fundy, North Minas Basin, i.e., Stewiacke (STW and S), Great Village (GRV and G), and Economy (ECO and E) rivers, were used to generate the cross types analyzed here (Fig. 1). Genetic data suggest that genetic differentiation between IBoF populations may be small (F_{ST} range = 0.01–0.04; Fraser et al. 2007), that gene flow between populations may be high (Fraser et al. 2007), and that populations may have similar numbers of differentially-expressed functional genes (Tymchuk et al. 2010). On the other hand, pair-wise DNA mitochondrial genetic differentiation (Φ_{ST}, ECO vs. STW = 0.0198, ECO vs. GRV = 0.4545, GRV vs. STW = 0.0587; Verspoor et al. 2002) and pair-wise DNA microsatellite genetic differentiation (F_{ST}, ECO vs. STW = 0.0938–0.0968, ECO vs. GRV = 0.0673, GRV vs. STW = 0.0345–0.0361; Tymchuk et al. 2010) suggest that there may be large genetic differences between some rivers. In addition, DNA microsatellite data suggest that the ECO and GRV populations, but not the STW population, have experienced genetic bottlenecks in the recent past (A.L.S. Houde, D.J. Fraser, P. O'Reilly, and J.A. Hutchings, unpublished data). Genetic bottlenecks suggest the loss of locus heterozygosity and, thus, a greater likelihood of heterosis in the first outbred generation (Tallmon et al. 2004).

Generation and recovery of 2003 parental cross types

Wild, age 1+ year salmon parr were collected by electrofishing in 2001 from STW, GRV, and ECO, and reared at the Coldbrook Biodiversity Facility, Coldbrook, Nova Scotia. Genotype information at 9 or more of 11 loci (*Ssa197*, *Ssa202*, O'Reilly et al. 1996; *SSsp1605*, *SSsp2201*,

Fig. 1. Location of the experimental river populations in the North Minas Basin region of the Inner Bay of Fundy. The bold line on the Economy River watershed represents a waterfall barrier to upstream passage of Atlantic salmon.



SSsp2210, *SSsp2213*, *SSsp2215*, *SSsp2216*, *SSspG7*, Paterson et al. 2004; *SsaD486*, and *SsaD144*, King et al. 2005) had been acquired previously, as described in O'Reilly and Harvie (2009).

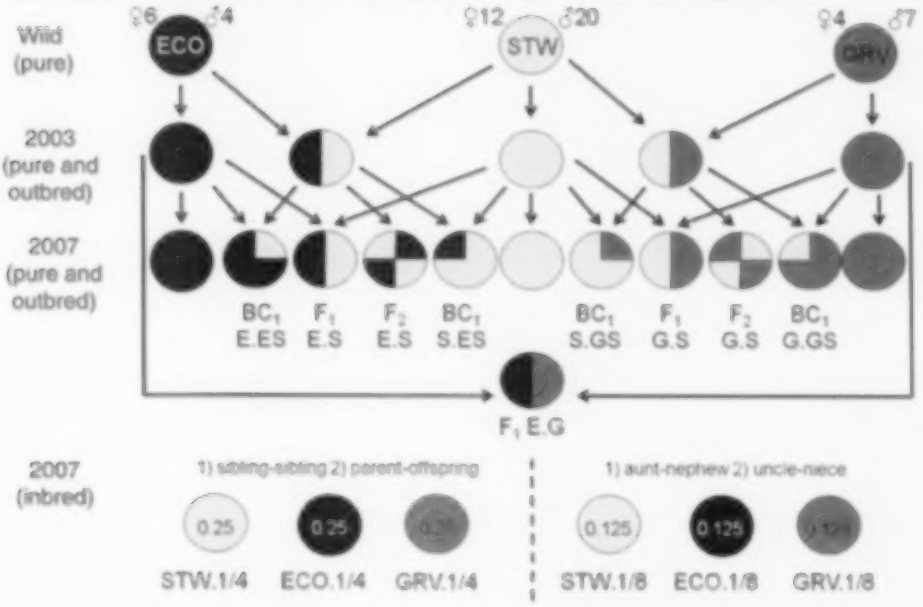
Using the wild fish as parents, families were generated in fall 2003 for pure (noninbred within-population cross types: ECO, GRV, and STW) and first-generation outbred (F_1 E.S and F_1 G.S: pure 1 × pure 2) cross types at the Mersey Biodiversity Facility, Milton, N.S. The offspring were pooled, transferred to Coldbrook, N.S., in July 2004, and raised to sexual maturity under common-environmental conditions (temperature, dissolved oxygen, pH) at different densities. An exclusion-based family assignment simulation in FAP 3.6 (Taggart 2007), using the information of known families (i.e., known female–male mated pairs) at five loci (i.e., *Ssa197*, *SSsp1605*, *SSsp2215*, *SSsp2216*, and *SSspG7*), determined that 99.8% of offspring could be unambiguously assigned to each family. The 2003 offspring were genotyped at these five microsatellite loci and assigned back to known families, using an Excel® Exclusion-based macro (Carolyn Harvie, Fisheries and Oceans Canada, Bedford Institute of Oceanography, Dartmouth, N.S., unpublished data). Only the offspring that matched the original wild parents at all five loci were accepted as candidate parents in the production of the next generation.

Generation of 2007 experimental cross types

Cross types were carried out within and among the three populations, using a combination of the adults recovered from the 2003 parental cross types and the original wild fish as parents (Fig. 2). The 18 cross types generated contained 3 pure (noninbred, within-population) cross types, 6 inbred cross types (inbreeding coefficients, $F = 0.125$ and 0.25 per within-population mating, assuming a base population inbreeding coefficient of $F = 0$, Wang et al. 2002), and 9 interpopulation outbred (hybrid) cross types (first-generation, second-generation, and back-cross outbred cross types). The original wild fish were used because the number of families from some of the 2003 parental cross types was low (e.g., ECO = four available families). To mitigate the potential confounding individual maternal and individual paternal representation of the families in comparing the cross types, the same 10 females and the same 10 males from a parental cross type, i.e., ECO, GRV, STW, F_1 E.S, and F_1 G.S, were used in a balanced design to generate 20 families per cross type.

Cross types were generated on 5 and 8 November 2007 at Coldbrook. Females and males were anaesthetized, using tricaine methanesulphonate (MS-222) for handling ease, and were later revived. All the eggs contained within each female were divided equally among the number of families that were to be generated using that female. The eggs were fertilized immediately, using a volume of milt proportional to the amount of eggs (~1 mL to 500 eggs), and left undisturbed for 90 s to permit fertilization. Water was then added and the eggs were allowed to fertilize for another 90 s. Each family was haphazardly placed into one of the six sections of different egg trays contained within an incubation trough.

Fig. 2. Experimental cross types within (pure and inbred) and among (outbred) rivers. Cross type symbols: ECO and E, Economy (black); GRV and G, Great Village (dark grey); and STW and S, Stewiacke (light grey). F_1, first-generation outbred; F_2, second-generation outbred ($F_1 \times F_1$); BC_1, back-cross outbred (pure $\times$ F_1); 1/4, inbreeding coefficient of 0.25; and 1/8, inbreeding coefficient of 0.125. Arrows represent the parental cross types; ♀, number of wild females; and ♂, number of wild males. The proportion of genes from any one population is reflected by the area of the circle in outbred cross types. The numbers within circles represent inbreeding coefficients (F). The phrases above the circles for inbred cross types are examples of the matings used to generate that inbreeding coefficient.



As per the Coldbrook egg-rearing protocol, all eggs were treated with formalin (625 ppm) for 20 min twice a week to prevent the spread of fungus from unfertilized and dead eggs to live eggs. In total, 247 families were produced at Coldbrook.

Measurement of early-life survival and fitness-related traits

We first measured egg survival (fertilization to eyed stage and eyed stage to hatch) and alevin survival (post-hatch until yolk sac was completely absorbed) as direct measures of early-life survival. We then measured seven traits that may influence body size and, thus, survival at later life stages (e.g., fry to adult) in salmonids (Metcalfe and Thorpe 1992; Pakkasmaa et al. 2001; Koskinen et al. 2002): development time to 50% hatch; egg diameter at eyed stage (307 degree-days); length at hatch; yolk sac volume at hatch; length at yolk sac absorption; specific growth rate and yolk sac conversion efficiency.

Eyed eggs from all cross types were transferred from Coldbrook to the Aquatron Facility, Dalhousie University (Halifax, N.S.) on 19 and 20 March 2008 (294 degree-days) because of rearing space constraints at Coldbrook. The transfer coincided with the development stage during which eggs can be safely transported without causing developmental harm (Purser and Forteath 2003). Because of an unforeseen technical problem at the Coldbrook Biodiversity Facility, 29 families exhibited 100% mortality, thus leaving 218 families at the Aquatron (Table 1). Owing to the mortality, individual maternal and individual paternal representation of the families was no longer balanced in comparing the cross types. At the Aquatron, the eggs were kept in modified Lee's® Kritter Keepers, perforated with 1.5" (3.81 cm) holes patched with pet screen to allow water flow, and divided into two sections (13.8 cm × 17 cm), using perforated plastic board. Coloured plastic beads (13 mm × 6 mm) with numerical identifiers were attached to the centre of each section. A family was haphazardly placed in a Kritter Keeper section and three Kritter Keepers occupied a 67.3 cm diameter × 45.7 cm height circular tank. The water temperature (nearest 0.1 °C) of each tank was recorded daily.

All dead and unfertilized eggs from the period at Coldbrook were removed on 21–23 March. We were unable to discern dead from unfertilized eggs, both of which represent different parental effects. For the period at the Aquatron, dead eggs and alevins were counted and removed daily at the same time of day from 24 March to 25 April for eggs (total of 33 days) and from 22 March to 19 May for alevins (total of 59 days). As the eggs hatched, the number of alevins was recorded daily at the same time of day from 19 March to 26 April. For families that contained large numbers of alevins, digital photographs were collected to precisely count alevins daily, using ImageJ version 1.38 (available from the Research Services Branch of the National Institutes of Health (US)). Development time at 50% hatch was measured in growing degree-days ($\Delta D = \Sigma$ °C per day) from the spawning date.

Digital photographs of the families were collected for the following: live egg counts and egg diameters on 22 and 23

Table 1. Number of families and number of individual parents per cross type for the Aquatron data.

Families		Total number of individuals		Number of individuals for the family compositions of F_1 and BC_1 outbred cross types			
Cross type	*N*	Females	Males	Females-group 1	Males-group 2	Females-group 2	Males-group 1
Pure cross types (females × males)							
ECO	17	9 (5)	10 (6)				
GRV	11	7 (2)	8 (5)				
STW	12	7 (0)	9 (2)				
Inbred cross types (females × males)							
ECO.1/4	6	5 (2)	5 (2)				
ECO.1/8	8	5 (1)	7 (5)				
GRV.1/4	5	5 (2)	3 (1)				
GRV.1/8	2	2 (1)	2 (1)				
STW.1/4	7	7 (0)	7 (0)				
STW.1/8	5	4 (0)	4 (0)				
F_1 outbred cross types (females group 1 × males group 2 and females group 2 × males group 1)							
E.G	15	15	14	8 (5)	7 (5)	7 (3)	7 (4)
E.S	14	14	14	8 (5)	8 (2)	6 (0)	6 (4)
G.S	16	16	16	8 (3)	8 (2)	8 (1)	8 (5)
BC_1 outbred cross types (females group 1 × males group 2 and females group 2 × males group 1)							
E.ES	16	16	15	8 (4)	7	8	8 (5)
G.GS	16	15	13	7 (2)	7	8	6 (4)
S.ES	16	16	16	7 (1)	7	9	9 (3)
S.GS	17	16	16	8 (0)	7	8	9 (3)
F_2 outbred cross types (females × males)							
E.S	16	8	8				
G.S	19	10	8				

Note: Total *N* for families = 218. Females were mated once per cross type except in the generation of pure and F_2 outbred cross types, in which the majority were mated twice. Numbers in parentheses are the number of wild parents. F_1 and BC_1 outbred cross types are expressed as group 1–group 2 in cross type column. For example, E.ES is composed of females–ECO (group 1) × males–F_1 E.S (group 2) and females–F_1 E.S (group 2) × males–ECO (group 1).

March; alevin total length (total length from the tip of the snout to the last trace of tail visible); yolk sac length, and yolk sac width at hatch on 13 April; and alevin total length at yolk sac absorption on 19 May, for 15 randomly chosen individuals. ImageJ was calibrated to the 6 mm beads in the Kritter Keeper sections for size measurements (nearest 0.1 mm). Yolk sac volume was calculated as yolk sac length × (yolk sac width)^2 × $\pi/6$ (Koskinen et al. 2002). Specific growth rate (G) was calculated as 100 [ln(length of unfed fry) – ln(length just after hatch)]/ΔD, and yolk sac conversion efficiency was calculated as (fork length at first feeding – 203 fork length just after hatch)/yolk sac volume (Fraser et al. 2010).

Analysis

Early-life history traits of families were analyzed for differences among pure and inbred cross types as a test of genetic effects due to inbreeding, and among pure and outbred cross types as a test of genetic effects due to outbreeding. Data were analyzed in R 2.9.0 (available from the R Project for Statistical Computing, www.r-project.org) and statistical significance was set at the $\alpha = 0.05$ level. Early-life history traits were first examined for nuisance effects, i.e., tray position/ tank effects and density effects (number of eggs per Kritter Keeper section), and for simple maternal effects, i.e., relationships with maternal length, using linear or generalized linear models and Pearson correlations (Table 2).

Model selection for significant effects

Forward step-wise model selection, using Akaike Information Criteria, was used to generate an ordered list of significant effects. Variables used for model selection were maternal ID, paternal ID, maternal environment, paternal environment, maternal cross type, paternal cross type, cross type, as well as variables for any significant nuisance effects or relationships with maternal length from previous tests. Parental environment referred to the captive (F_1 captive) and wild environmental origin of the parents. Linear models were used for normal data and weighted binomial generalized linear models were used for proportional data. If a binomial model was overdispersed, the model was reconstructed as a quasi-binomial model. Nonsignificant effects, starting with nonsignificant interactions, were removed one at a time after an analysis of variance of a linear model, or an analysis of deviance of a binomial or quasi-binomial model.

Individual maternal effects (i.e., maternal ID) and individual paternal effects (i.e., paternal ID), if retained by the selection process, were examined for significant differences among parental cross types (i.e., ECO, F_1 E.S, GRV, F_1

Table 2. Final model structures for analysing nuisance effects and simple maternal effects for early-life history traits.

Trait	Error*	Link	Position/tank ID	Density	Maternal length†
Egg survival					
At Coldbrook	Quasi-binomial	Logit	GLM, ANODEV	GLM, ANODEV	GLM, Pearson
At day 33	Quasi-binomial	Logit	GLM, ANODEV	GLM, ANODEV	GLM, Pearson
Alevin survival					
At day 59	Quasi-binomial	Logit	GLM, ANODEV	GLM, ANODEV	GLM, Pearson
Development time					
At 50% hatch	Normal	Identity	ANOVA	Pearson	LM, Pearson
Size					
Egg diameter	Normal	Identity	ANOVA	Pearson	LM, Pearson
Length at hatch	Normal	Identity	ANOVA	Pearson	LM, Pearson
Yolk sac volume	Normal	Identity	ANOVA	Pearson	LM, Pearson
Length at yolk absorption	Normal	Identity	ANOVA	Pearson	LM, Pearson
Energy conversion					
Specific growth rate	Normal	Identity	ANOVA	Pearson	LM, Pearson
Yolk sac conversion efficiency	Normal	Identity	ANOVA	Pearson	LM, Pearson

Note: GLM, generalized linear model; ANODEV, analysis of deviance of GLM. LM, linear model; ANOVA, analysis of variance; Pearson, Pearson correlation.

*Quasi-binomial, error correction for overdispersion, i.e., originally binomial models that contained residual scaled deviance degrees of freedom that were roughly not equal to the residual degrees of freedom.

†Pearson correlation was examining the correlation of individual maternal effect sizes (from the GLM or LM) and maternal length.

G.S, and STW) and parental environments (i.e., captive and wild). Significant differences among the parental cross types and parental environments were determined by plotting the 95% confidence intervals (CIs) of the effect sizes.

Cross type effects in simple models

Early-life history traits were examined for differences among cross types, using simple models. Any parental effect variable (e.g., maternal ID, paternal ID, maternal environment, and paternal environment), except maternal length, in the final model was removed and replaced with a single cross type effect variable (cross type) to generate the simple model. In addition, any variables of tray position or tank ID in the final model were modeled as random effects in the simple model. Linear, binomial, or quasi-binomial models were used for models that did not include random effects. For models that did include random effects, linear mixed-effects models, using the function lmer in the lme4 package of R, were used for normal data. Proportional data were logit-transformed to increase normality (Crawley 2005), using logit in the *car* package of R, before being used in linear mixed-effects models. All mixed-effects models used restricted maximum likelihood estimation and Laplace approximations to estimate parameter values.

Significant differences among the effect sizes for cross type were determined by plotting the CIs of the effect sizes. For mixed-effects models, CIs were generated by Markov Chain Monte Carlo sampling of the posterior distribution of effect size estimates, using mcmcsamp with 5000 samples and HPDinterval functions in the lme4 package.

Cross type effects in mixed-effects models

If individual maternal effects or individual paternal effects were generated by model selection along with a cross type effect, there were missing effect sizes for some of the cross types. This was most likely due to a loss of statistical power because of the loss of families at Coldbrook that resulted in the loss of information on females and males within cross types. To obtain cross type effect estimates, individual maternal and paternal effects were treated as two random intercepts in mixed-effects models. Tray position and individual tank effects, if present in model selection, were also treated as random intercepts. Any significant variables that remained from model selection were treated as fixed effects in the mixed model. Significant differences among the effect sizes for cross type were determined by plotting the CIs of the effect sizes.

Results

Although nuisance factors, such as tank effects and density, had a significant influence on some early-life history traits (Table 3), few were selected in the final models when they were included in the list of variables for model selection (Table 4). In addition, the model selection procedure revealed that most early-life history traits were significantly influenced by maternal effects. Furthermore, in the simple models, there were some significant differences between pure cross types and those resulting inbred and outbred cross types (Fig. 3). However, there were no significant cross type-level differences between inbred and pure cross types, or between outbred and pure cross types, once individual parental effects had been incorporated into mixed-effects models. Asterisks denote significant differences (i.e., non-overlapping confidence intervals) and "ns" denotes non-significant differences (i.e., overlapping confidence intervals). Individual parental effects extracted from the final model were grouped to examine confidence intervals for the parental cross type and parental environment result columns. Cross type effect column displays the confidence interval

Table 3. Nuisance effects examined and relationship with maternal length for early-life history traits.

Trait	Position/tank ID, p	Density, p	Maternal length, p
Egg survival			
At Coldbrook	<0.001*	0.159	0.002*, +
At the Aquatron (day 33)	<0.001*	0.004*, –	0.267
Alevin survival			
At day 59	0.141	0.003*, +	0.272
Development time			
At 50% hatch	0.042*	<0.001*, 0.27	0.161
Size			
Egg diameter	<0.001*	<0.001*, 0.14	<0.001*, 0.82
Length at hatch	<0.001*	<0.001*, 0.09	0.050*, 0.28
Yolk sac volume	<0.001*	<0.001*, 0.20	<0.001*, 0.80
Length at yolk absorption	<0.001*	<0.001*, –0.24	0.117
Energy conversion			
Specific growth rate	0.042*	0.032*, –0.15	–0.776
Yolk sac conversion efficiency	0.010*	<0.001*, –0.32	<0.001*, –0.67

Note: Displayed are p-values and Pearson correlations or the direction of the relationship. Asterisks denote significant p-values.

results for the cross type effect in a mixed-effects model (different than the final model) that treated individual parental effects as random effects.

Egg survival

We found no evidence of significant inbreeding or outbreeding effects on egg survival at Coldbrook (fertilization to eyed stage), although a cross type effect was detected in model selection. However, upon examination of the cross type CIs, there were no significant egg survival differences between inbred and pure cross types, outbred and pure cross types, or inbred and outbred cross types in mixed-effect models (Fig. 4). While there was a positive correlation between maternal length and egg survival, when maternal length was included in the list of variables for model selection, it was not selected. In addition, there was a significant effect of tray position in the incubation trough on egg survival at the Coldbrook. The egg mortality may have been caused by vibrations generated at the base of the incubation trough by the formalin dispenser, which could have disrupted egg development (Purser and Forteath 2003).

We found no evidence for differential egg survival at the Aquatron at day 33 (eyed stage to hatch) among cross types. While there was a significant negative correlation between initial egg density and egg survival, when initial egg density was included in the list of variables for model selection, it was not selected.

Alevin survival

There was no evidence for differential alevin survival at day 59 (hatched until yolk sac absorption) among cross types. However, small but significant maternal cross type effects were detected. Alevins with ECO mothers had higher survival (95% CI difference; 1.67 ± 1.00%) than alevins with F_1 G.S mothers (Fig. 5). While there was a significant positive correlation between initial egg density and alevin survival, when initial egg density was included in the list of variables for model selection, it was not selected.

Development time at 50% hatch

We found no evidence for differential development time at 50% hatch among cross types. However, significant maternal environment effects were detected, with offspring of captive mothers requiring more time (95% CI difference; 9.71 ± 6.21 degree-days) to hatch than offspring of wild mothers (Fig. 5). While there was a significant positive correlation between initial egg density and the development time at 50% hatch, individual maternal effects (i.e., maternal ID) were more important than density effects in model selection.

Size of eggs, alevins at hatch, yolk sac, and alevins at yolk sac absorption

We found no evidence of significant inbreeding or outbreeding effects on size traits. A cross type effect was detected for all size traits in model selection, however, upon examination of the cross type CIs, there were no significant size trait differences between inbred and pure cross types, outbred and pure cross types, or inbred and outbred cross types in mixed-effect models (Fig. 4). However, significant maternal cross type effects were detected (Fig. 5). Offspring with F_1 G.S mothers had larger egg diameter (95% CI difference; F_1 E.S = 0.30 ± 0.17, GRV = 0.31 ± 0.17 mm), yolk sac volume (ECO = 15.75 ± 7.54, F_1 E.S = 10.83 ± 7.11, GRV = 11.99 ± 7.11 mm^3), and length at yolk absorption (F_1 E.S = 2.00 ± 1.11, GRV = 2.38 ± 1.11 mm), than offspring with ECO (yolk sac volume only), F_1 E.S, and GRV mothers. In addition, significant paternal cross type effects were detected for egg diameter only. Offspring with STW fathers had a smaller egg diameter (F_1 E.S = 0.09 ± 0.05, GRV = 0.08 ± 0.05, F_1 G.S = 0.12 ± 0.05 mm) than offspring sired by the remaining paternal cross types, except for offspring with ECO fathers.

Table 4. Model selection results, parental effects, and cross type effects for early-life history traits.

Trait	Final model	Maternal cross type	Maternal environ.	Paternal cross type	Paternal environ.	Cross type effect
Egg survival						
At Coldbrook	Tray position + maternal ID + paternal ID + cross type	ns	ns	ns	ns	*
At the Aquatron (day 33)	Tank ID + maternal ID + paternal ID	ns	ns	ns	ns	
Alevin survival						
At day 59	Maternal ID	*	ns			
Development time						
At 50% hatch	Maternal ID + initial egg density	ns	*			
Size						
Egg diameter	Maternal length + maternal ID + paternal ID + cross type	*	ns	*	ns	ns
Length at hatch	Maternal length + maternal ID + paternal ID + cross type	ns	ns	ns	ns	ns
Yolk sac volume	Maternal length + maternal ID + paternal ID + cross type	*	ns	ns	ns	ns
Length at yolk absorption	Maternal ID + paternal ID + cross type	*	ns	ns	ns	*
Energy conversion						
Specific growth rate	Maternal cross type	*				
Yolk sac conversion efficiency	Maternal length + maternal cross type	ns				

These size trait models defined maternal length as the first variable because of the strong correlations between maternal length and size traits, except length at yolk absorption. In addition, there were significant individual tank effects and a significant positive correlation between initial egg density and size traits. However, tank ID and initial egg density were not included in the list of variables for model selection because the individual tank effects probably reflected the haphazard placement of different sized families (e.g., smaller captive vs. larger wild mother egg diameters) within tanks while the density effect reflected the correlation of maternal length with size traits given that maternal length was also correlated with initial egg density (Pearson correlation, $r = 0.493$, $p = \ll 0.001$).

Specific growth rate and yolk sac conversion efficiency

We found no evidence for differential specific growth rate and yolk sac conversion efficiency among cross types. However, for both specific growth rate and yolk sac conversion efficiency, there were significant maternal cross type effects detected. Offspring with STW mothers experienced a faster specific growth rate (95% CI difference; ECO = 0.022 ± 0.013, GRV = 0.021 ± 0.014) than offspring produced by ECO and GRV mothers (Fig. 5). For yolk sac conversion efficiency, the offspring of STW mothers expressed a higher yolk sac conversion efficiency (ECO = 0.026 ± 0.054, F_1 E.S = 0.030 ± 0.050, GRV = 0.023 ± 0.054, F_1 G.S = 0.038 ± 0.049) than the offspring of other maternal cross types, although this difference was not significant.

The model for yolk sac conversion efficiency defined maternal length as the first variable, similar to the analysis of size traits, because of the strong negative correlation between yolk sac conversion efficiency and maternal length. In addition, there were significant individual tank effects and significant negative correlations between initial egg density and energy conversion traits. However, tank ID and initial egg density were not included in the list of variables for model selection for the same reasons as they were not included for size trait model selection.

Discussion

Our objective was to evaluate the relative fitness of inbred and inter-population outbred cross types, using three small neighbouring populations of endangered Atlantic salmon under common-environmental conditions in captivity. A salient feature of our work is that no significant differences between inbred and pure cross types, outbred and pure cross types, or inbred and pure cross types were detected among the fitness-related traits under examination. However, most traits were influenced by parental effects that needed to be incorporated into our analyses before potential differences among cross types could be adequately tested.

Parental effects

Individual parental effects were more important than cross type effects in explaining the variance among families. That is, using model selection, individual parental effects, maternal ID and sometimes paternal ID, would appear before a cross type effect, cross type. In addition, parental effects present in the cross types gave, in some instances, the false impression of significant cross type differences when parental effects were not incorporated into the models. Furthermore, these parental effects were present in cross types that had been generated by considerable numbers of females and males (8–10 individual females or males per cross type). Sometimes parental effects may be ignored in the comparison of cross types generated by several females and males because they are believed not to have a large influence of the mean value of the cross type (e.g., Gharrett et al. 1999; McGinnity et al. 2003; Gilk et al. 2004). The present work can be added to the growing number of studies that have detected individual paternal effects in early-life history traits of salmon (e.g., Pakkasmaa et al. 2001; Petersson and Järvi 2007; Wedekind et al. 2008), a finding that challenges the traditional assumption that there are few individual paternal effects in salmonid early-life history traits (Miller et al. 2004; Smoker et al. 2004; Green 2008).

The individual-specific parental effects that were detected in the present study have also been detected in other studies

Fig. 3. Cross type effect size estimates using simple models. Displayed are 95% confidence intervals, (*a*) egg survival at Coldbrook, (*b*) egg survival at the Aquatron (day 33), (*c*) alevin survival at day 59, (*d*) development time at 50% hatch, (*e*) egg diameter, (*f*) length at hatch, (*g*) yolk sac volume, (*h*) length at yolk absorption, (*i*) specific growth rate, (*j*) yolk sac conversion efficiency. Numbers at the top are the sample sizes for the cross types. Cross type symbols: ECO and E, Economy; GRV and G, Great Village; and STW and S, Stewiacke; F_1, first-generation outbred; F_2, second-generation outbred ($F_1 \times F_1$); BC_1, backcross outbred (pure $\times$ F_1); 1/4, inbreeding coefficient of 0.25; and 1/8, inbreeding coefficient of 0.125.

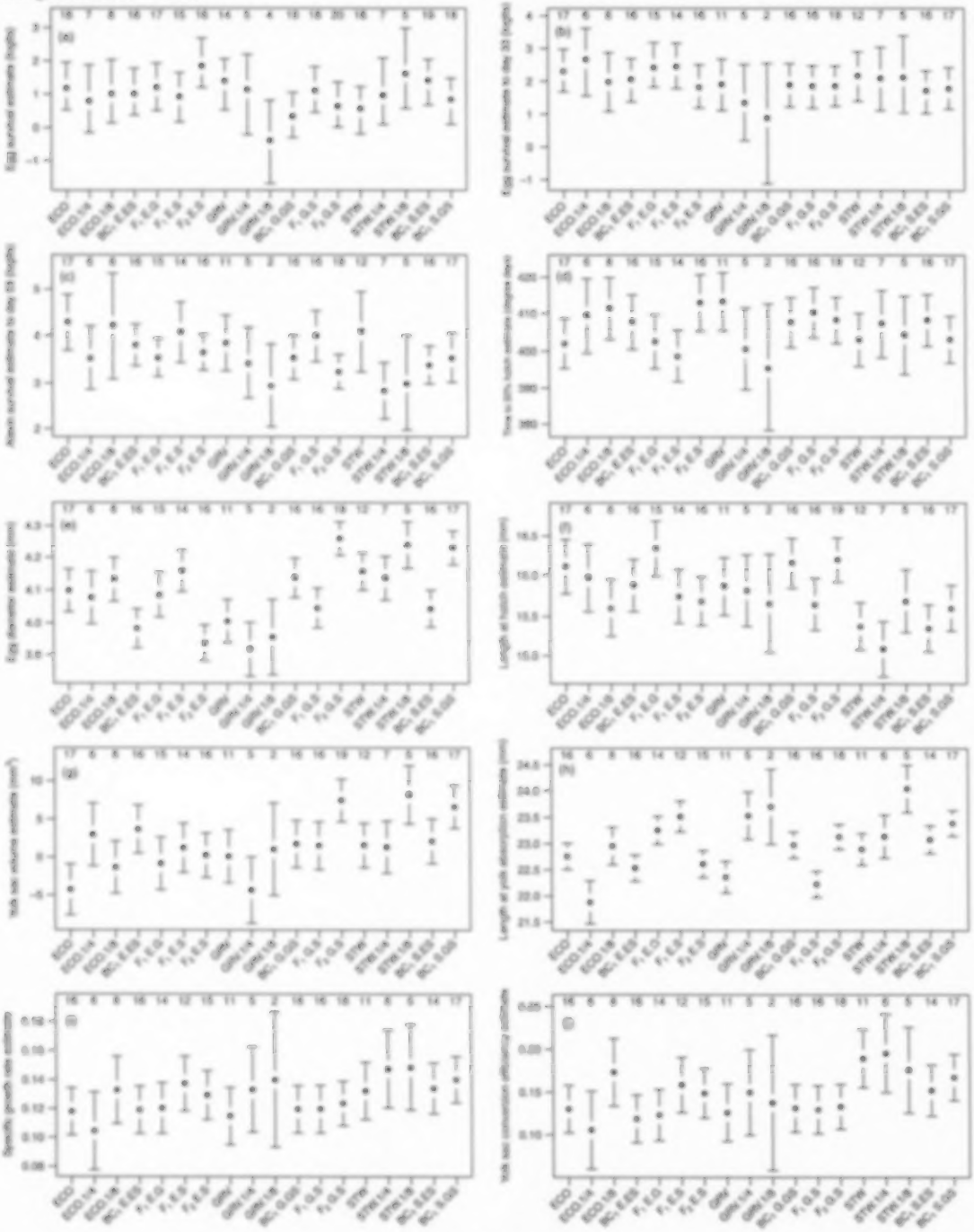
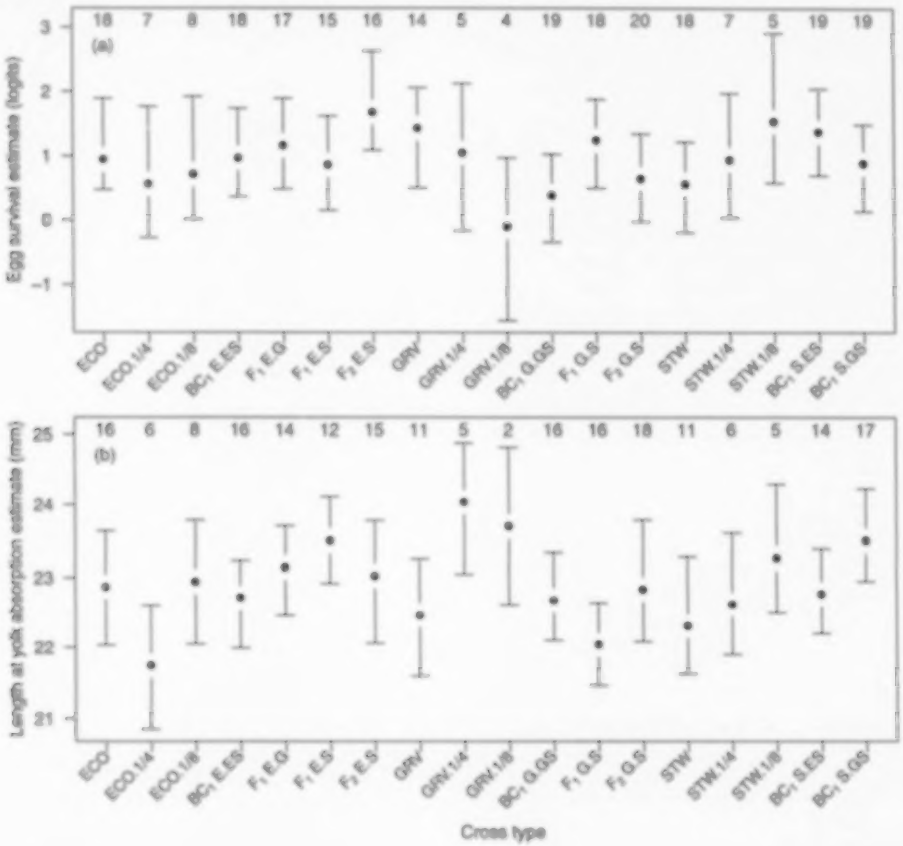


Fig. 4. Cross type effect sizes estimates using mixed-effects models. Displayed are 95% confidence intervals, (*a*) egg survival at Coldbrook, and (*b*) length at yolk absorption. Cross type symbols: ECO and E, Economy; GRV and G, Great Village; and STW and S, Stewiacke; F_1, first-generation outbred; F_2, second-generation outbred ($F_1 \times F_1$); BC_1, backcross outbred (pure $\times$ F_1); 1/4, inbreeding coefficient of 0.25; and 1/8, inbreeding coefficient of 0.125.



of salmonids. Egg and alevin survival, for example, are known to be affected by individual maternal effects (e.g., Nagler et al. 2000; Vandeputte et al. 2002; Smoker et al. 2004). However, these same studies did not detect individual paternal effects on egg survival. In the case of egg survival at Coldbrook, individual paternal effects may have been detected because individual fathers differ in their ability to fertilize eggs (e.g., sperm velocity, Gage et al. 2004; match to female major histocompatibility alleles, Yeates et al. 2009) and because unfertilized eggs were indistinguishable from dead eggs (representing two different parental effects) in our analyses. Nevertheless, others have detected individual paternal effects on the survival of fertilized eggs in salmonids (e.g., Wedekind et al. 2001; Granath et al. 2004; Wedekind et al. 2008).

Offspring size traits are known to be affected by maternal effects, such as body length (e.g., Beacham and Murray 1985; Bailey and Loudenslager 1986; Berg et al. 2001), and by paternal effects of smaller effect (e.g., Refstie and Steine 1978; Pakkasmaa et al. 2001; Gilbey et al. 2005). In our study, offspring energy conversion traits were not affected by individual maternal effects, contrary to the findings of Heath et al. (1993), while specific growth rate was not affected by maternal length, a finding similar to that reported by Gilbey et al. (2009). Furthermore, there was a significant negative correlation of yolk sac conversion efficiency with maternal length. It is possible that the energy contained within yolk reserves was directed towards mass growth rather than towards length growth in the offspring of larger females, given that all offspring were approximately the same length at the time of release (mean ± 1 SD, 22.9 ± 2.0 mm). This is consistent with research that has found a positive relationship between offspring weight gain and maternal length (e.g., Ojanguren et al. 1996; Vandeputte et al. 2002).

Differences between the offspring of captive and wild parents

There may have been other genetic or epigenetic differences between captive and wild parents that may have affected offspring traits. The "captive" parents were born in captivity, and had spent one generation in captivity (F_1 captive), whereas the "wild" parents were born in the wild, collected as juveniles, and had spent the remainder of their lives in captivity. The difference in birth and rearing environments

Fig. 5. Individual parental effects estimates grouped by parental cross type and parental environment. Displayed are 95% confidence intervals.(*a*) egg survival at Coldbrook, (*b*) egg survival at the Aquatron at the Aquatron (day 33), (*c*) alevin survival at day 59, (*d*) development time at 50% hatch, (*e*) egg diameter, (*f*) length at hatch, (*g*) yolk sac volume, (*h*) length at yolk absorption, (*i*) specific growth rate, (*j*) yolk sac conversion efficiency. Parental cross type symbols: ECO and E, Economy; GRV and G, Great Village; and STW and S, Stewiacke; and F_1, first-generation outbred. Parental environment symbols are C, captive parent; and W, wild parent.

may have created different maternal and other epigenetic effects between captive and wild parents (Kawecki and Ebert 2004). The one additional generation of domestication selection might have caused genetic differences to have arisen between captive and wild parents because of selection resulting from mate choice in natural spawning environments, compared with the lack thereof in artificial spawning circumstances (Fleming 1994; Wedekind 2002; Pitcher and Neff 2007) or because of the increased expression of rare deleterious alleles in captive populations relative to those found in the wild (Frankham 2008). The above differences may translate into a smaller egg size produced by captive adults relative to those produced by wild adults when examined in the laboratory environment (Heath et al. 2003; Jonsson et al. 1996). However, in the present study there was no significant parental environment effect on egg diameter. There were also no significant parental environment effects on egg or alevin survival.

Regarding the other fitness-related traits examined here, there were no genetic or epigenetic effects that have not been documented previously, with the exception that offspring produced by wild mothers required fewer degree-days to reach the 50% hatch stage. The difference between offspring of both captive and wild mothers was up to 5 degree-days, which would translate to a difference of approximately 1–2 days in the wild, which may have minimal biological significance. One additional consideration is that wild parents may have developed as embryos at colder temperatures in the wild than did captive parents in captivity, which may have been manifested by different maternal or epigenetic effects (see Kawecki and Ebert 2004). In other words, the offspring of wild parents may be "programmed" to develop at faster rate per degree-day than the offspring of captive parents.

Risks of inbreeding vs. outbreeding

After accounting for the influences of maternal length and (or) individual parental effects, inbred and outbred cross types did not differ significantly from their respective pure cross types at a multitude of early-life history traits (165 comparisons per trait).

The lack of significant genetic differentiation between inbred, outbred, and pure cross types in survival may be attributable, in part, to the comparatively benign rearing conditions of the laboratory relative to those that would be experienced by individuals in the wild (Miller 1994; Crnokrak and Roff 1999; Bijlsma et al. 2000). In addition, the outbred cross types, ideally, should have been tested in their pure parental local environments to evaluate the potential for a loss of local adaptation, which is one mechanism by which outbreeding depression can be generated (Kawecki and Ebert 2004; McClelland and Naish 2007). By contrast, one considerable advantage associated with laboratory studies for these early-life stages is the increased accuracy and precision with which survival can be estimated. Furthermore, there may be additional factors in the wild, such as size-based dispersal (McGinnity et al. 1997), which might result in a nonrandom shift of some fish out of the sampling area; such sampling biases can be eliminated in the laboratory. An additional consideration is that the magnitudes of detrimental outbreeding effects documented in a laboratory setting are likely to be more severe in the wild (Edmands 2007).

Notwithstanding the laboratory environment caveats, we note that inbreeding depression has been documented in rainbow trout (*Oncorhynchus mykiss*) in the laboratory (Kincaid 1976*a*, 1976*b*; Gjerde et al. 1983). We are also cognisant of the fact that inbreeding coefficients are a function of current consanguineous matings and inbreeding history (Allendorf and Luikart 2007). Thus, our assumption of a base population inbreeding coefficient of $F = 0$ might not have been valid for ECO and GRV, given their recent population bottlenecks (see Wang et al. 2002). Yet, if ECO and GRV populations were more inbred than the STW population, there was certainly no indication of this in our results: significantly greater inbreeding depression was not detected in the pure or inbred cross types for ECO and GRV populations relative to the pure cross type or inbred cross types of the STW population. On the other hand, assuming greater fixations of deleterious recessive alleles from previous inbreeding for ECO and GRV, inbreeding depression may not have been detected for these two populations because the magnitude of difference in traits between pure and inbred cross types is expected to be much higher in STW relative to ECO and GRV (Allendorf and Luikart 2007).

Significant genetic differences between outbred and pure cross types may also not have resulted from outbreeding in our study because of small genetic differentiation and potentially high gene flow between the Inner Bay of Fundy populations (see Materials and Methods for F_{ST} values). That is, the mixing of populations that are similar genetically and have a history of interbreeding may not express outbreeding depression or heterosis (Edmands and Timmerman 2003; Kawecki and Ebert 2004; Tallmon et al. 2004).

Interestingly, there were differences observed between the offspring of F_1 outbred parents and those of pure parents. For example, F_1 G.S mothers produced offspring that were ~0.3 mm larger in egg diameter than F_1 E.S and GRV mothers. Also, there were paternal cross type effects for egg diameters. That is, F_1 E.S and F_1 G.S fathers produced offspring that were larger in egg diameter than the offspring of STW fathers. These egg size enlargements could be a product of heterosis, given that larger size is associated with higher early-life fitness (Wallace and Aasjord 1984; Beacham and Murray 1985; Einum and Fleming 1999). However, these enlargements, if biologically meaningful, could equally be considered outbreeding depression if smaller egg size in STW salmon represents an adaptive response to the local environment (cf., Hutchings 1991; Taylor 1991; Garcia de Leaniz et al. 2007). However, we are unaware of any ma-

Maternal cross type
Maternal environment
Paternal cross type
Paternal environment
(a)
(b)
(c)
(d)
(e)
Egg survival estimate (logit)
Egg survival estimate to day 33 (logit)
Alevin survival estimate to day 59 (logit)
Time to 50% hatch estimate (degree days)
Egg diameter estimate (mm)
ECO
F1 E.S.
GRV
F1 G.S.
STW
C
W
Parental cross type or parental environment

Maternal cross type
Maternal environment
Paternal cross type
Paternal environment
(a)
(b)
(c)
(d)
(e)
Length at hatch estimate (mm)
Yolk sac volume estimate (mm³)
Length at yolk absorption estimate (mm)
Specific growth rate estimate
Yolk sac conversion efficiency estimate
ECO
F1 E.S
GRV
F1 G.S
STW
C
W
Parental cross type or parental environment

jor differences in the three populations' habitats that might account for a smaller size being favoured in the Stewiacke River.

Overall, there appear to be no fitness-related advantages or disadvantages to inbreeding or outbreeding these three populations, in this common-environment laboratory setting and at the early-life stages examined. These results should be interpreted with caution since the relative life-time fitness of these crosses should be measured in more natural settings or, ideally, the local environments. In addition, without prior knowledge on egg size selection in the local environment of these populations, it cannot be determined whether the changes in egg size are a fitness-related advantage or disadvantage. Our work identifies a need to undertake comparative studies of the survival and fitness-related traits between cross types in the natural environment.

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A comparison of polymorphism of genetic markers and population sample sizes required for mixed-stock analysis of sockeye salmon (*Oncorhynchus nerka*) in British Columbia

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Abstract: We evaluated two questions: (*i*) do microsatellites require larger population baseline sample sizes than single nucleotide polymorphisms (SNPs) to allow the accuracy provided by the microsatellites in genetic stock identification (GSI) applications to be expressed, and (*ii*) do less genetically distinct populations require larger population baseline sample sizes than more distinct populations to improve population-specific accuracy in GSI applications? Forty-six SNP loci were surveyed in 40 populations of sockeye salmon (*Oncorhynchus nerka*) over 16 regions from southern and central British Columbia and were split into two groups: the top 23 SNPs evaluated for stock identification for British Columbia sockeye salmon and the poorest 23 nuclear SNPs. Fourteen microsatellites were surveyed and split into two groups, with loci from the top 7 loci for stock identification accuracy assembled in one group, and the remaining 7 microsatellites assigned to a second group. SNPs and microsatellites with lower stock identification power required larger population sample sizes to allow expression of stock identification potential. To achieve the same level of population-specific accuracy, SNPs required fewer individuals to be sampled in a population than did microsatellites. Less genetically distinct populations required larger population sample sizes to achieve a given level of accuracy in estimated stock compositions.

Résumé : Nous considérons deux questions. Est-ce qu'il faut des échantillons plus importants de données démographiques de base dans le cas des microsatellites que dans celui des polymorphismes mononucléotidiques (SNP) pour permettre l'expression de la précision des microsatellites dans leur utilisation pour l'identification génétique des stocks (GSI)? Est-ce que les populations moins distinctes génétiquement requièrent de plus grands échantillons de données de base que les populations plus distinctes pour améliorer la précision spécifique à l'espèce dans les problèmes de GSI? Nous avons examiné 46 locus SNP dans 40 populations de saumons rouges (*Oncorhynchus nerka*) dans 16 régions du sud et du centre de la Colombie-Britannique et les avons séparés en deux groupes, les 23 SNP estimés les meilleurs pour l'identification des stocks de saumons rouges de Colombie-Britannique et les 23 SNP moins performants. Nous avons aussi examiné 14 microsatellites et les avons séparés en deux groupes, les sept locus les plus précis pour l'identification des stocks dans un groupe et les sept autres microsatellites dans l'autre groupe. Les SNP et les microsatellites à puissance d'identification des stocks plus faible requièrent des échantillons démographiques plus importants pour permettre l'expression de leur potentiel d'identification des stocks. Afin d'atteindre le même niveau de précision pour les différentes populations, les SNP nécessitent un échantillonnage de moins d'individus dans la population que les microsatellites. Les populations moins distinctes génétiquement requièrent des échantillons démographiques plus importants pour atteindre un niveau donné de précision dans les estimations de composition des stocks.

[Traduit par la Rédaction]

Introduction

In genetic stock identification (GSI) applications, a baseline of populations potentially contributing to mixed-stock fishery samples is developed, and then, genetic differences among these populations are used to provide estimates of stock composition of samples collected from fisheries. The estimated stock compositions that are generated, are subject to at least two sources of error. The first is sampling error, both in the baseline populations and mixed-fishery samples. Sampling error occurs for the baseline populations when the allele frequencies estimated for a particular genetic marker in a population differ from the actual frequencies in the population. As the number of fish surveyed in the population increases, sampling error generally decreases as a result of the estimated allele frequencies being closer to the actual population allele frequencies. Sampling error can also occur in the fishery sample, as the stock proportions in the fishery

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sample collected may differ from the true proportions of fish in the fishery. As with baseline population sampling error, increasing the size of the sample from the fishery may tend to reduce this source of error. The second source of error occurs when the genetic markers surveyed in the baseline are applied to estimate stock compositions in the fishery sample. Few genetic markers provide 100% discrimination among populations in a complex baseline, and thus some level of error is expected in estimating stock compositions. This error arises because a finite number of loci are sampled, and there is a lack of differentiation among baseline populations in the genetic markers surveyed. This error can be potentially decreased by adding additional informative markers to increase the resolution among baseline populations. In evaluating stock identification effectiveness among different types of genetic markers, it is important to understand that the estimated accuracy of stock composition in a mixture will be influenced both by sampling error in allele frequencies in the baseline populations, and the degree of genetic differentiation among populations expressed for the markers surveyed.

A question arises as to the appropriate number of individuals to analyze in a population to minimize sampling variance in the estimate of allele frequencies for loci with widely divergent numbers of alleles. Kalinowski (2004), in an analysis involving simulated genetic data, reported that little benefit was gained in increasing baseline population sample size above 100 fish for loci displaying 2–128 alleles, although he did suggest that the lack of benefit of higher sample size seemed paradoxical for highly polymorphic loci. Winans et al. (2004), in an analysis of Columbia River steelhead (*Oncorhynchus mykiss*), surveyed 32 allozymes and five microsatellites, with the microsatellites containing 8–21 alleles per locus, and they analyzed approximately 50 fish per population. Through simulation analysis, they concluded that sampling more than 50 fish per population produced little improvement in accuracy of estimated stock compositions, and that the more heterozygous microsatellites did not require or benefit from having larger sample sizes than less polymorphic allozyme loci, with 72% of the 32 allozymes examined having 3–4 alleles per locus. Studies incorporating microsatellites in genetic stock identification applications or individual identification for Atlantic salmon (*Salmo salar*) are usually based upon fewer than 100 individuals sampled per population in the baseline (Koljonen et al. 2005; Glover et al. 2010; Griffiths et al. 2010). Based upon the previously mentioned studies, one could conclude that only 50–100 fish are required to be surveyed in a population to minimize sampling error in estimation of allele frequencies, even for loci containing up to 128 alleles.

Two main classes of genetic markers are currently in use in GSI applications for Pacific salmon. The first class of markers is single nucleotide polymorphisms (SNPs), where SNP loci typically display two alleles per locus. The second class of markers is microsatellites (also known as single tandem repeats (STRs)), where microsatellite loci typically display from 2–150 alleles per locus. The GSI effectiveness of each class of markers is of considerable current interest, and a recent report noted that comparisons of current and future costs and performance of microsatellites and SNPs will be required before an objective selection of a single approach in GSI applications might be justified (Pacific Salmon Commission 2008). The second source of GSI error estimation is key in this evaluation, and to properly assess the relative effectiveness of the two classes of markers, evaluations should only be conducted when the first source of error (sampling error associated with allele frequency estimation) has been minimized. Is it realistic to conclude that sampling error for population allele frequency estimation for loci containing up to 128 alleles per locus is minimized when only 50–100 fish in the population have been analyzed? If this assumption is incorrect, then inadequate baseline sampling of populations may unduly influence reported GSI accuracy of different classes of genetic markers.

The common North American species of Pacific salmon differ in their genetic distinctiveness among populations. Sockeye salmon (*O. nerka*) are the most distinct, with an F_{ST} value of 0.097 observed for 14 microsatellites over 299 populations with a Pacific Rim distribution (Beacham et al. 2006*a*). Chinook salmon (*O. tshawytscha*) are next most distinct, with an F_{ST} value of 0.063 observed for 13 microsatellites over 325 populations with a Pacific Rim distribution (Beacham et al. 2006*b*). Coho salmon (*O. kisutch*) rank next in genetic distinctiveness, with an F_{ST} value of 0.058 observed for 17 microsatellites over 318 populations with a largely North American distribution (Beacham et al. 2011). Chum salmon (*O. keta*) are among the less distinct species, with an F_{ST} value of 0.033 observed for 14 microsatellites over 381 populations with a Pacific Rim distribution (Beacham et al. 2009*a*). Population genetic distinctiveness, and thus the potential for GSI estimation errors, clearly differs among the Pacific salmon species. If populations to be discriminated in GSI applications are quite distinct, then perhaps higher levels of sampling error for allele frequency estimation can be tolerated, as errors in estimates of population allele frequencies should be much less than differentiation in allele frequencies among populations. Conversely, if populations to be separated in GSI applications are less distinct, increased emphasis could be placed on reducing sampling error associated with allele frequency estimation, in order not to obscure differentiation from the genetic markers used. Given these scenarios, it may be unreasonable to assume that there should be a fixed sample size target for the baseline populations in GSI applications across species and populations within species. It may be that for the more difficult GSI applications, those in which genetic differentiation among populations is limited, larger baseline population sample sizes may be required to provide the maximum differentiation possible with the genetic markers employed.

In the current study, we evaluate the effect of variation in population sample size in GSI applications for 40 populations of sockeye salmon in British Columbia. We also evaluate the effect of population genetic differentiation on the accuracy of estimates of stock composition, using suites of SNPs and microsatellites for each population included in the evaluation. The following key questions were investigated. (*i*) Do microsatellites require larger population baseline sample sizes than SNPs to improve accuracy in GSI applications? (*ii*) Do less genetically distinct populations require larger population baseline sample sizes than more distinct populations to improve accuracy in GSI applications?

Materials and methods

Collection of DNA samples and laboratory analysis

Tissue samples were collected from mature sockeye salmon from 40 populations with varying levels of genetic distinctiveness (Table 1; Fig. 1). Samples were preserved in 95% ethanol and sent to the Molecular Genetics Laboratory at the Pacific Biological Station (Nanaimo, British Columbia). DNA was extracted from the tissue or scale samples using a variety of methods, including a chelex resin protocol outlined by Small et al. (1998), a QIAGEN 96-well DNeasy® procedure, or a Promega Wizard SV96 Genomic DNA Purification system. Once the extracted DNA was available, variation at SNP and microsatellite loci was surveyed. Forty-six SNP loci were surveyed and were split into two groups: the top 23 SNPs (*One-MHC2–190*, *One-MHC2-251*, *One-HPAL-99*, *One-GPH-414*, *One-U503-170*, *One-RAG3-93*, *One-ZP3B-52*, *One-ACBP-79*, *One-TF-EX3-182*, *One-RF-112*, *One-STR07-190*, *One-HGFA-100*, *One-HGFA-100*, *One-HCS71–220*, *One-U401–224*, *One-C1259*, *One-LEI-87*, *One-TF-EX10–750*, *One-STC-410*, *One-GPDH-360*, *One-ALDOB-135*, *One-SEPP*, and *One-U404-229*) that produced the highest accuracy in estimated population stock composition for British Columbia sockeye salmon (defined as T23) (Beacham et al. 2010), and the poorest 23 nuclear SNPs (*One-GPDH2–211*, *One-PLNS-107*, *One-U508-533*, *One-OTS213-181*, *One-HSP47*, *One-U301-92*, *One-VIM-569*, *One-HPAL-436*, *One-PIP-1-PIP3*, *One-P53-576*, *One-RAG1-103*, *One-U504-141*, *One-PRL2*, *One-CTGF-301*, *One-ZNF-61*, *One-SERPIN-104*, *One-IL8R-362*, *One-RF-295*, *One-GHII-2461*, *One-RH2OP-395*, *One-KPNA-422*, *One-U502-167*, *One-MARCKS-241*, and *One-E2*) (B23, Beacham et al. 2010). DNA was amplified with one negative control on each 96- or 384-well plate. Amplification reactions consisted of 1 μL DNA and 4 μL cocktail consisting of TaqMan genotyping mastermix, primers, probes, and water, with thermal cycling conducted with an initial denaturation of 10 min at 95 °C followed by 50 cycles of 95 °C for 15 s and 60 °C for 90 s. After polymerase chain reaction (PCR) amplification, the plates were read on an ABI Prism 7900HT Sequence Detection System by one individual using Sequence Detection Software version 2.3 (Applied Biosystems, Foster City, California) to generate scatter plots that depicted the amount of each allele-specific probe that bound to the PCR product of each individual.

Fourteen microsatellites were surveyed and split into two groups. The seven microsatellites that when evaluated produced the highest accuracy in estimated stock compositions were combined into a group (top 7) (T7; *Ots100*, *Ots103*, *Ots108*, *Oki10*, *Oki16*, *Oki29*, *Omy77*; Beacham et al. 2010). The remaining seven microsatellites, which when evaluated produced lower accuracy in estimated stock compositions, were combined in a group (bottom 7) (B7; *One8*, *Oki1a*, *Oki1b*, *Oki6*, *One8*, *Ots2*, *Ots3*, *Ots107*; Beacham et al. 2010). Microsatellites were initially size fractionated in denaturing polyacrylamide gels using an ABI 377 automated DNA sequencer, and genotypes were scored by Genotyper 2.5 software (Applied Biosystems) using an internal lane sizing standard. Later in the study, microsatellites were size fractionated in an ABI 3730 capillary DNA sequencer, and genotypes were scored by GeneMapper software 3.0 (Applied Biosystems) using an internal lane sizing standard. Allele scores derived from Genotyper or GeneMapper were verified by either one or two laboratory personnel. Allele identification between the two sequencers was standardized by analyzing approximately 600 individuals on both platforms and converting the sizing in the gel-based data set to match that obtained from the capillary-based set.

Estimation of stock composition in single-population samples

Observed allele frequencies were available for the 46 SNPs and 14 microsatellites surveyed in the 40 populations evaluated (Beacham et al. 2010). All loci were considered to be in Hardy–Weinberg equilibrium (microsatellites, Beacham et al. (2006*a*); SNPs, T. Beacham, B. McIntosh, and C. MacConnachie unpublished data), and expected genotypic frequencies were determined from the observed allele frequencies. Using observed allele frequencies and applying CBayes (Neaves et al. 2005) to generate multilocus genotypes, we simulated sample sizes of 400 individuals for each SNP locus and 600 individuals for each microsatellites locus for each of the 40 populations. Estimation of stock composition of single-population mixtures was conducted with ONCOR (Kalinowski et al. 2007; Anderson et al. 2008). Genotypic frequencies were determined for each locus in each population and were used to estimate stock composition of simulated single-population samples. The Rannala and Mountain (1997) correction to baseline allele frequencies was used for ONCOR analyses to avoid the occurrence of fish in the mixed sample from a specific population having an allele not observed in the baseline samples from that population, with accuracy and precision of the stock composition estimates calculated by bootstrapping 100 times over baseline population sample sizes and a mixture size of 200 fish. The effect of population sample size on average accuracy of estimated stock compositions for both population-specific and regional estimates was investigated for SNP population sample sizes ranging from 20 to 400 individuals in increments of 20 individuals, with samples of the appropriate size created by sampling each 400 individual population sample without replacement. For microsatellites, population sample sizes ranged from 20 to 600 individuals in increments of 20 individuals, with samples of the appropriate size created by sampling each 600 individual population sample without replacement. Population and regional estimates of stock composition were determined for each of the 40 populations with each of the two suites of SNPs (T23, B23) and two suites of microsatellites (T7, B7). Mean accuracy for each population sample size was determined as the average estimate across all 40 populations. Allocations to individual baseline populations were summed to provide estimates of stock compositions for regional stock groups (Table 1). An asymptotic regression model of the form $Y = a - b\exp(-cX)$ was fitted to the mean accuracy data, where Y represents the predicted percentage accuracy, a represents the asymptotic percentage accuracy, b and c represent fitted variables, and X represents population sample size. The asymptotic regression model was fitted to the accuracy and population sample size data with Labfit curve fitting software (da Silva and Silva 2007), and estimates of population sample size required for 90% and 95% of asymp-

Table 1. Regions, populations surveyed within regions, and mean pairwise F_{ST} estimates for 40 populations of sockeye salmon from 16 regions in British Columbia estimated for the top 23 SNPs (T23) evaluated for stock identification for British Columbia sockeye salmon and the poorest 23 diploid SNPs (B23).

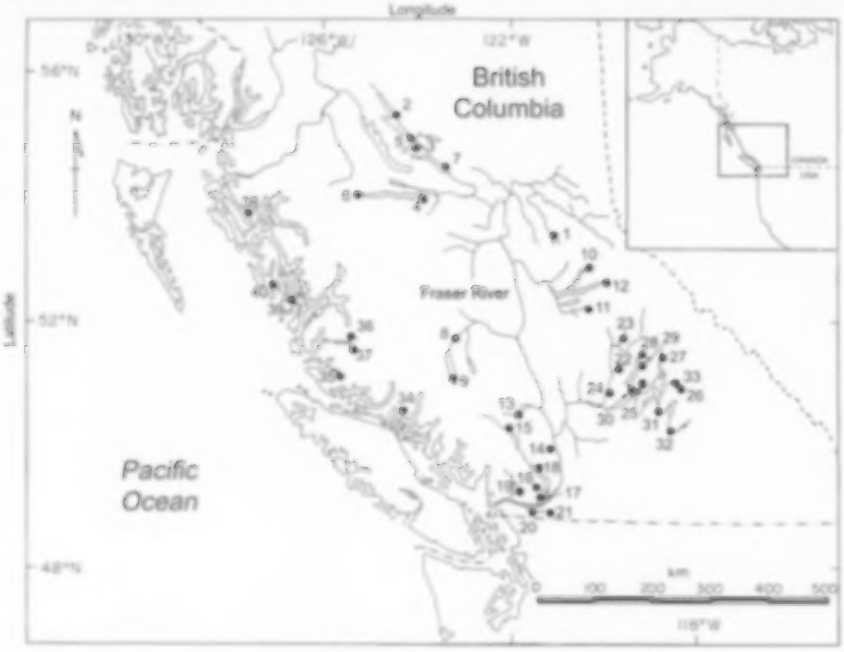
Region	Population	SNP T23	SNP B23	Micro T7	Micro B7
Upper Fraser	1) Bowron Lake	0.1268	0.0832	0.0691	0.0811
Early Stuart	2) Takla Lake	0.1407	0.0735	0.0511	0.0543
Early Stuart	3) Trembleur Lake	0.1545	0.0754	0.0550	0.0477
Stuart/Nechako	4) Stellako River	0.0959	0.0490	0.0519	0.0572
Stuart/Nechako	5) Middle River	0.1504	0.0798	0.0528	0.0512
Stuart/Nechako	6) Nadina River	0.1773	0.0766	0.0643	0.0570
Stuart/Nechako	7) Pinchi Creek	0.1826	0.0910	0.0771	0.0962
Chilko	8) Chilko River	0.1332	0.0633	0.0578	0.0649
Chilko	9) Chilko Lake south	0.1262	0.0536	0.0544	0.0585
Quesnel	10) Mitchell River	0.1111	0.0650	0.0996	0.0805
Quesnel	11) Upper Horsefly	0.1029	0.0702	0.0560	0.0640
Quesnel	12) Blue Lead Creek	0.1214	0.0579	0.0633	0.0783
Canyon	13) Gates Creek	0.1746	0.0936	0.1034	0.1751
Canyon	14) Nahatlatch River	0.1303	0.0999	0.0663	0.0795
Harrison	15) Birkenhead River	0.1535	0.0760	0.0609	0.0699
Harrison	16) Weaver Creek	0.1666	0.0723	0.0722	0.0637
Harrison	17) Harrison River	0.1465	0.0624	0.0575	0.0675
Harrison	18) Big Silver Creek	0.1288	0.0672	0.0757	0.0731
Lower Fraser	19) Pitt Lake	0.1424	0.0616	0.0498	0.0494
Chilliwack	20) Cultus Lake	0.2506	0.1679	0.1210	0.1546
Chilliwack	21) Chilliwack Lake	0.1816	0.1634	0.1224	0.0835
North Thompson	22) Fennell Creek	0.0896	0.0677	0.0625	0.0611
North Thompson	23) Raft River	0.1415	0.0530	0.0643	0.0624
North Thompson	24) North Thompson River	0.2380	0.0793	0.1208	0.0995
Shuswap (early)	25) Scotch Creek	0.0884	0.0472	0.0600	0.0540
Shuswap (early)	26) Eagle River (early)	0.1243	0.0533	0.0658	0.0576
Shuswap (early)	27) Seymour Creek	0.1082	0.0529	0.0591	0.0549
Shuswap (early)	28) Upper Adams River	0.1294	0.0740	0.0697	0.0879
Shuswap (early)	29) Cayenne Creek	0.1324	0.0810	0.1067	0.1224
Shuswap (late)	30) Lower Adams River	0.1015	0.0500	0.0458	0.0460
Shuswap (late)	31) Lower Shuswap River	0.1060	0.0535	0.0482	0.0516
Shuswap (late)	32) Middle Shuswap River	0.1111	0.0567	0.0503	0.0513
Shuswap (late)	33) Eagle River (late)	0.1051	0.0525	0.0536	0.0454
South Coast	34) Phillips River	0.0821	0.0926	0.0581	0.0564
Long Lake	35) Canoe Creek	0.1786	0.0447	0.0645	0.0795
Owikeno	36) Washwash River	0.1331	0.0514	0.0627	0.0746
Owikeno	37) Neechanz River	0.1366	0.0441	0.0629	0.0622
Central Coast	38) Devon Lake	0.2533	0.0955	0.0899	0.1215
Central Coast	39) Tankeeah River	0.1452	0.0695	0.0537	0.0504
Central Coast	40) Kent Lake	0.2669	0.0916	0.1026	0.1153

Note: Fourteen microsatellites were surveyed and split into two groups, with seven loci providing more accurate estimates of stock composition combined in one group (T7, 276 alleles), whereas the other group contained seven loci that provided less accurate estimates of stock composition (B7, 142 alleles). Location of populations is illustrated in Fig. 2, by number.

totic accuracy for each of the two suites of SNPs and two suites of microsatellites determined.

To evaluate whether less genetically distinct populations required larger population baseline sample sizes than more distinct populations to improve accuracy in GSI applications, we first calculated Weir and Cockerham's (1984) pairwise population F_{ST} estimates for each suite of loci (SNP T23, B23; microsatellite T7, B7) over all populations with FSTAT version 2.9.3.2 (Goudet 1995). The level of difficulty in identifying a particular population in mixed-stock fishery analysis will depend upon its genetic distinctiveness with respect to other populations for the suite of genetic markers incorporated. As an index of genetic distinctiveness, for each of the four suites of loci, we subsequently sorted in a second analysis all pairwise F_{ST} estimates for each population in ascending order, and determined the mean of the five smallest F_{ST} estimates for each of the 40 populations for each suite of loci. Five populations were chosen to illustrate trends in accuracy with respect to population sample size. These populations ranged in genetic distinctiveness and were as follows: Devon Lake (quite distinct), Nadina River, Stellako River, Eagle River early run, and Neechanz River (less distinct). The accuracy of population-specific estimates was plotted as a function of population sample size to illus-

Fig. 1. Map indicating locations of 40 sockeye salmon populations surveyed in British Columbia, Canada, modified from Beacham et al. (2010). Population names are indicated in Table 1.



trate how accuracy of stock composition estimates changed for these populations as a function of changing population sample size, with the stock compositions estimates derived from applying the 40-population baseline. This portion of the analysis centered subsequently on the B23 suite of SNPs and B7 suite of microsatellites. For each population in each of these suites, the population sample size required to attain 95% of the accuracy achieved at the 400-individual level for SNP B23 and 600-individual level for microsatellite B7 was estimated. Genetically distinct populations may reach asymptotic identification accuracy at smaller population sample sizes than less distinct populations, and the relationship between the F_{ST} index and the population sample size required to achieve 95% of final accuracy was evaluated.

Results

Comparisons within SNPs

The T23 suite of SNPs displayed substantial genetic differentiation among the 40 populations evaluated, with an overall F_{ST} estimate of 0.151 (Table 2). The level of genetic differentiation incorporated by these 23 SNPs resulted in an average single-population accuracy of estimated stock composition of 85% with only 40 fish sampled per population. With 100 fish sampled per population, average accuracy increased to 90% per population, and at 300 fish sampled per population, an average accuracy of 94% for population-specific stock compositions was achieved (Fig. 2*a*). Asymptotic accuracy was estimated to be 95.4%, and was observed at a sample size of 400 fish per population. Analysis of 400 fish per population would not typically be conducted in a survey of SNP variation, as the incremental gain in accuracy diminished rapidly after the first 100 fish in a population had been sampled (Fig. 2*a*). In fact, 90% of asymptotic accuracy was achieved at a sample size of 43 fish per population, and 95% of asymptotic accuracy was achieved at a sample size of 115 fish per population (Table 3).

Table 2. Number of independent alleles, total alleles, and F_{ST} estimate for suites of SNP and microsatellite markers across 40 populations of sockeye salmon in British Columbia.

Marker	Independent alleles	Total alleles	Overall F_{ST}
SNP-T23	23	46	0.151 (0.018)
SNP-B23	23	46	0.073 (0.006)
Micro-T7	269	276	0.078 (0.014)
Micro-B7	135	142	0.089 (0.011)

Note: Suites of markers were outlined as in Table 1.

In regional estimation of stock composition incorporating the T23 suite of SNPs, a level of accuracy of 95% was achieved at a sample size of 40 individuals, with an asymptotic accuracy estimated at 98%, which was observed at a sample size of approximately 200 individuals (Fig. 2*b*). As would be expected, accuracy of estimated regional stock compositions was higher than those of individual populations at all population sample sizes. Population sample size required to achieve 90% of asymptotic accuracy was estimated at only 11 individuals, and 32 individuals were estimated to be required to achieve 95% of asymptotic accuracy (Table 3).

The B23 suite of SNPs displayed less than half of the genetic differentiation observed with the T25 suite, with an

Fig. 2. Mean population accuracy over 40 sockeye salmon populations in British Columbia versus population sample size for suites of (*a*) SNPs (T23, filled triangle, (▲); B23, filled circle, (●)) and (*b*) microsatellites (T7, filled square, (■); B7, filled diamond, (◆)) as outlined in Table 1. The sample size at which 95% of asymptotic accuracy is achieved is indicated. Mean regional accuracy for (*c*) SNPs and (*d*) microsatellites is also indicated (broken lines).

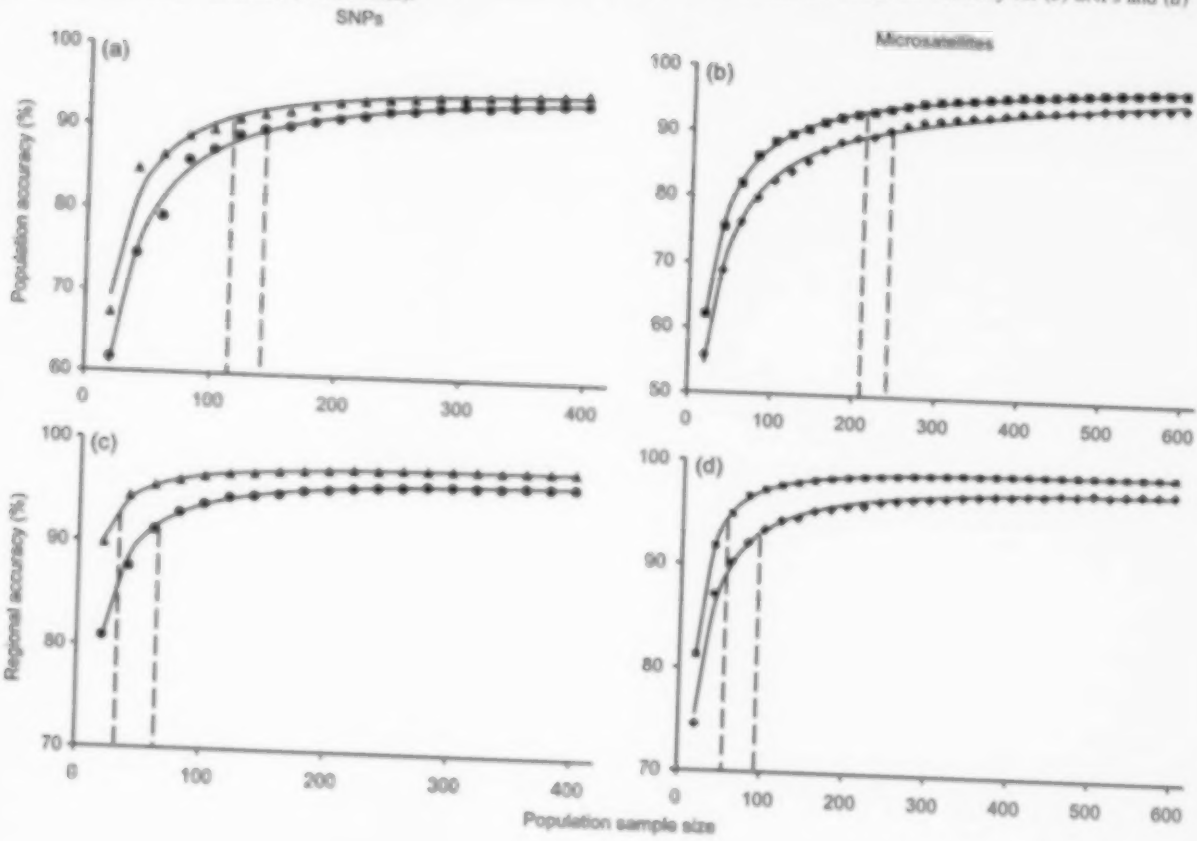


Table 3. Parameter estimates from fitting the asymptotic regression equation $Y = a - b\exp(-cX)$ to mean population percentage accuracy results for both populations and regions, where Y represents the predicted percentage accuracy, a represents the asymptotic percentage accuracy, b and c represent fitted variables, X represents population sample size, and r^2 is proportion of variance accounted for by the regression.

Marker	*a*	*b*	*c*	r^2	90%	95%
SNPs-population						
T23	95.36	14.50	0.0097	0.9958	43	115
B23	94.28	17.36	0.0092	0.9944	66	141
SNPs-region						
T23	97.51	14.02	0.0325	0.9731	11	32
B23	96.03	18.94	0.0214	0.9869	31	64
Microsatellites-population						
T7	98.20	17.78	0.0061	0.9990	97	210
B7	95.64	27.00	0.0071	0.9973	145	242
Microsatellites-region						
T7	99.01	35.70	0.0363	0.9840	35	54
B7	97.45	16.10	0.0127	0.9849	40	94

Note: Population sample size estimates at 90% and 95% of asymptotic accuracy are also indicated.

overall F_{ST} estimate of 0.073 (Table 2). As expected, the B23 suite of SNPs provided less accurate estimates of population-specific composition at all population sample sizes compared with the T25 suite of SNPs. Accuracy of estimated population-specific compositions at a sample size of 40 individuals was 75%, 10% lower than observed with the T23 suite (Fig. 2*a*). However, the differential in accuracy between the two suites of SNPs decreased rapidly with increasing population sample size. With 100 fish sampled per population, average accuracy increased to 87%, a 3% differential with the T23 suite of SNPs. With 160 individuals sampled per population, the average accuracy increased to 90%, a 2% differential with the T23 suite. Asymptotic accuracy was estimated at 94.3%, and was observed at a sample size of about 400 fish per population. A sample size of 66 individuals were estimated to be required to attain 90% of asymptotic accuracy, with 142 individuals estimated to be required for achieving 95% of asymptotic accuracy. Increasing population sample size from 40 individuals had a more prolonged response in the B23 suite of SNPs. Sample size required to achieve 90% of asymptotic accuracy was 1.53 times higher for the B23 suite compared with the T23 suite, but only 1.23 times higher for achieving 95% of asymptotic accuracy. Although all SNPs surveyed had only two alleles per locus, SNPs with lower genetic differentiation displayed lower population-specific accuracy, and required larger population sample sizes (less sampling error in allele frequencies) to allow expression of stock identification potential.

Regional estimation of stock composition incorporating the B23 suite indicated that a 88% level of accuracy was achieved with a population sample size of 40 individuals, with an asymptotic accuracy of 96.0% (Table 3). Sample sizes were required to be at least twice as large to attain 90% and 95% levels of asymptotic regional accuracy for the B23 suite compared with the T23 suite.

Comparisons within microsatellites

The T7 suite of microsatellites displayed considerable genetic differentiation among the 40 populations evaluated, with an overall F_{ST} estimate of 0.078, and with an average of 39 alleles per locus observed (Table 2). The application of these seven loci resulted in an average single-population accuracy of estimated stock composition of 75% with 40 fish sampled per population. An average accuracy of 94% was achieved at a population sample size of 240 individuals, with an asymptotic accuracy of 98.2% (Table 3), which was achieved at a population sample size of in excess of 600 individuals (Fig. 2*a*). The incremental gain in accuracy diminished rapidly after the first 200 fish in a population had been sampled (Fig. 2*a*). Accordingly, 90% of asymptotic accuracy was achieved at a sample size of 97 fish per population, and 95% of asymptotic accuracy was achieved at a sample size of 210 fish per population (Table 3).

In regional estimation of stock composition incorporating the T7 microsatellites, a level of accuracy of 92% was achieved at a sample size of 40 individuals, with an asymptotic accuracy estimated at 99.0%, which was observed at a sample size of approximately 300 individuals (Fig. 2*b*). As with the SNPs, accuracy of estimated regional stock compositions was higher than those of individual populations at all population sample sizes. Population sample size required to achieve 90% of asymptotic accuracy was estimated at 35 individuals, and 55 individuals were estimated to be required to achieve 95% of asymptotic accuracy (Table 3).

The B7 suite of microsatellites displayed a similar level of genetic differentiation as did the T7 suite (B7, F_{ST} = 0.089; T2, F_{ST} = 0.078), but an average of only 20 alleles per locus were observed at these seven loci (Table 2). The B7 suite of microsatellites provided less accurate estimates of population-specific composition at all population sample sizes compared with the T7 microsatellites, and required larger population sample sizes to attain levels of accuracy comparable with the T7 suite of microsatellites. For example, accuracy of estimated population-specific compositions at a sample size of 40 individuals was 68%, 7% lower than the T2 microsatellites (Fig. 2*a*). With 100 fish sampled per population, average accuracy increased to 83%, a 6% differential with the T7 microsatellites. Asymptotic accuracy was estimated at 95.6%, and was projected to require in excess of 600 individuals per population to be sampled. A sample size of 145 individuals were estimated to be required to attain 90% of asymptotic accuracy for the B2 microsatellites, with 242 individuals estimated to be required for achieving 95% of asymptotic accuracy. Similar to the SNPs, microsatellites with lower stock identification power (lower accuracy in estimated stock compositions) required larger population sample sizes (less sampling error in allele frequencies) to allow expression of stock identification potential.

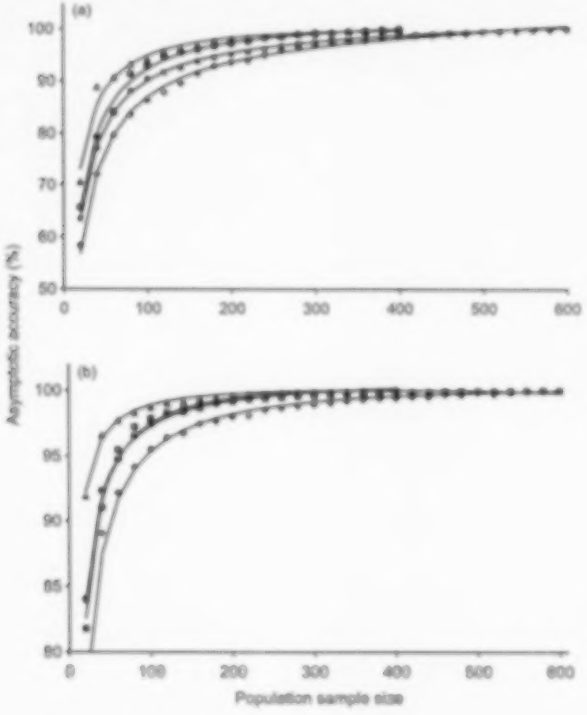
Regional estimation of stock composition incorporating the B7 microsatellites indicated that a 87% level of accuracy was achieved with a population sample size of 40 individuals, with an asymptotic accuracy of 97.5% (Table 3), which was achieved at a population sample size of about 460 individuals (Fig. 2*b*). Higher sample sizes were typically required to attain 90% and 95% levels of asymptotic regional accuracy for the B7 microsatellites compared with the T7 microsatellites (Table 3).

Comparisons between SNPs and microsatellites

Population asymptotic accuracy was similar among all four suites of genetic markers evaluated, ranging from 94.3% for the B23 SNPs to 98.2% for the T7 microsatellites. The levels of accuracy observed were attained from 46 total alleles for each suite of the B23 and T23 SNPs, 142 alleles for the B7 microsatellites, and 276 alleles for the T7 microsatellites (Table 2).

As expected, the greatest differential in estimated population-specific accuracy occurred at the smaller population sample sizes. With only 40 fish sampled in a population, the accuracy of stock compositions from the T23 SNPs was already at 89% of asymptotic accuracy, but only 77% of asymptotic accuracy for the T7 microsatellites (Fig. 3*a*). With a 100 fish population sample, the T23 SNPs produced an average population-specific accuracy of 94% of the asymptotic accuracy, compared with an average of 90% of asymptotic accuracy for the T7 microsatellites. An increase of population sample size to 200 fish resulted in an average of 98% of asymptotic population accuracy for the T23 SNPs, and an average of 95% for the T7 microsatellites. At a population size of 300 individuals, average population accuracy was greater than 99% of asymptotic accuracy for the

Fig. 3. Percentage of asymptotic stock correct assignment accuracy for populations (*a*) and regions (*b*) versus population sample size for suites of SNPs (T23, filled triangle, (▲); B23, filled circle, (●)) and microsatellites (T7, filled square, (■); B7, filled diamond, (◆)) as outlined in Table 1.



T23 SNPs, and an average of 97% for the T7 microsatellites. Although application of the T23 SNPs and T7 microsatellites resulted in similar asymptotic accuracy, the T7 microsatellites required larger sample sizes to have the population differentiation capability expressed to the same degree as the T23 SNPs. In this application, 90% of asymptotic accuracy was achieved at a population sample size of 43 individuals for the T23 SNPs and 97 individuals for the T7 microsatellites (Table 3). In a more stringent comparison, requiring expression of 95% of asymptotic accuracy, 115 individuals were required to be sampled in a population for the T23 SNPs, compared with 210 for the T7 microsatellites.

The lower resolution B23 SNPs and B7 microsatellites displayed the same trends in accuracy with respect to population sample size as did the higher resolution T23 and T7 suites of markers. For example, at a population sample size of 40 individuals, the accuracy of stock compositions from the B23 SNPs was at 79% of asymptotic accuracy, but only 72% of asymptotic accuracy for the B7 microsatellites (Fig. 3*a*). With a 100 fish population sample, the B23 SNPs produced an average population-specific accuracy of 93% of the asymptotic accuracy, with an average of 86% of asymptotic accuracy for the B7 microsatellites. The B7 microsatellites consistently required larger sample sizes to have the population differentiation capability expressed to the same degree as the B23 SNPs. For example, 90% of asymptotic accuracy was achieved at a population sample size of 66 individuals for the B23 SNPs and 145 individuals for the B7 microsatellites (Table 3). Comparable values for expression of 95% of asymptotic accuracy were 142 individuals sampled in a population for the B23 SNPs and 242 individuals for the B7 microsatellites. The general results indicated that to achieve the same level of population-specific accuracy, the SNPs, which have only 2 alleles per locus, clearly required fewer individuals to be sampled in a population than did the microsatellites, which could display over 40 alleles per locus.

Trends in accuracy of regional stock estimates were quite similar to those of population-specific estimates. Considerably higher sample sizes were required to attain 90% and 95% levels of asymptotic regional accuracy for the microsatellites compared with the SNPs (Fig. 3*b*; Table 3).

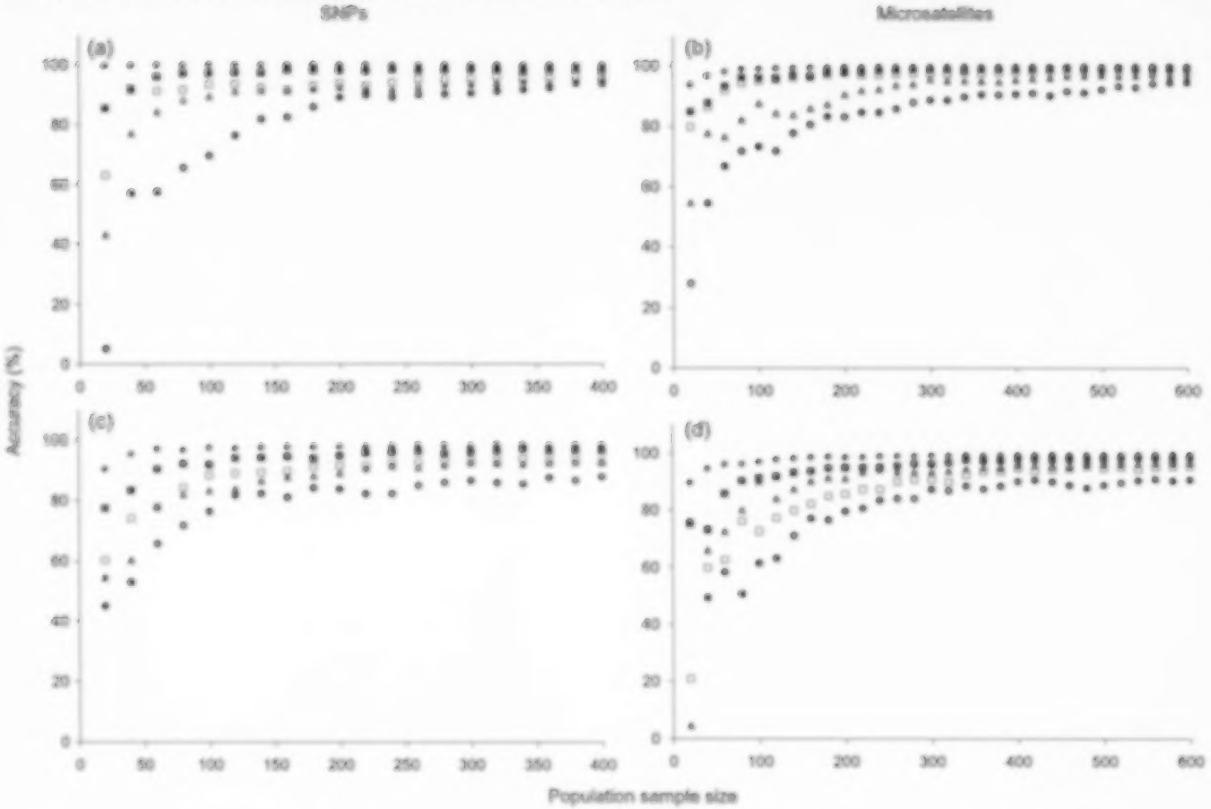
Population genetic differentiation and accuracy of estimated stock composition

Genetic differentiation of the 40 populations evaluated in the study varied considerably. Genetically distinct populations included Gates Creek (pairwise F_{ST} estimates ranged from 0.09 to 0.17), Cultus Lake (0.12–0.25), Chilliwack Lake (0.08–0.18), and Devon Lake (0.09–0.25), with these populations generally distinct at all suites of markers evaluated (Table 1). Other populations were less distinct and thus more challenging to identify in stock identification applications, such as Trembleur Lake (0.05–0.15), Phillips River (0.06–0.09), Eagle River early run (0.05–0.12), and Neechanz River (0.04–0.14). Given this level of variation in population genetic distinctiveness, the key question evaluated in this portion of the study was whether less genetically distinct populations require larger population baseline sample sizes than more distinct populations to improve accuracy in GSI applications.

Five populations with a range of genetic distinctiveness were chosen to illustrate the effect of baseline sample size variation on accuracy of population-specific estimates of stock composition. Devon Lake was a distinct population (average lowest pairwise F_{ST} value across four marker suites was 0.0698). The Nadina River (0.0231), Stellako River (0.0058), and Eagle River early (0.0100) populations were of intermediate distinctiveness, and the Neechanz River (0.0037) population was of lower distinctiveness. The application of the T23 SNPs to estimation of stock composition for the five populations resulted in accuracy of estimation of stock composition above 77% accuracy at a population sample size of 40 individuals in four of the five populations (Fig. 4*a*), limiting the scope for subsequent improvements in accuracy. The fifth population, Neechanz River, was estimated with an accuracy rate of 57%. Increasing population sample size to 200 individuals in this population generally resulted in a consistent increase in accuracy to 89%, after which increasing population sample size resulted in muted gains in accuracy. For the other four populations, only limited gains in accuracy were observed for population sample sizes in excess of 100 individuals.

The application of the lower power B23 SNPs resulted in a wider variation in estimation accuracy for a population sample size of 40 individuals (53%–96%) (Fig. 4*c*). Accuracy of estimated stock compositions in this case was more

Fig. 4. Percentage accuracy versus population sample size for the Devon Lake (filled diamond, ◆), Nadina River (filled square, ■), Stellako River (filled triangle, ▲), Eagle River (early run), open square, (□)), and Neechanz River (filled circle, ●) populations for suites of SNPs (*a*, T23; c, B23) and microsatellites (*b*, T7; d, B7) as outlined in Table 1.



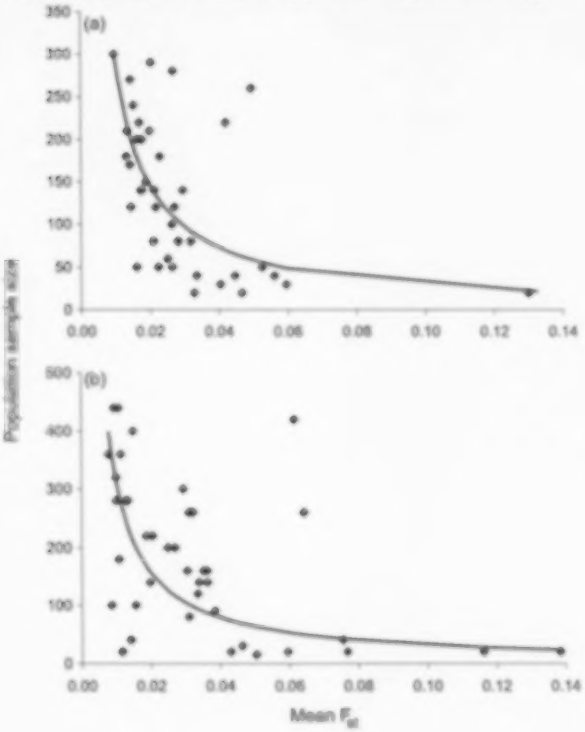
sensitive to population sample size. Accuracy of estimated stock compositions for populations that were initially poorly estimated (Neechanz River 53%, Stellako River 60%) at a population sample size of 40 individuals increased to 84% and 89%, respectively, at population sample sizes of 200 individuals. Increases in accuracy of estimated stock compositions were limited above a sample size of 200 individuals for all populations.

The accuracy of estimated stock compositions observed from application of the T7 microsatellites ranged from 55% to 97% at a population sample size of 40 individuals (Fig. 4*b*). Accuracy of estimated stock compositions of the two populations more difficult to identify (Neechanz River, Stellako River) increased consistently from 55% and 78%, respectively, at a population sample size of 40 individuals to 88% and 94%, respectively, at a population sample size of 280 individuals. Subsequent increases in the accuracy of stock composition estimates were limited for all populations after a population sample size of 300 individuals.

Application of the final suite of markers evaluated, the B7 microsatellites, resulted in a wide variation in accuracy of estimated stock compositions (49% to 95%) at a population sample size of 40 individuals (Fig. 4*d*), much like the B23 SNPs. Accuracy of estimated stock compositions for the two populations that were initially poorly estimated (Neechanz River, Eagle River) increased from 49% and 60%, respectively, at a population sample size of 40 individuals to 88% and 94%, respectively, at a population sample size of 360 individuals. The analysis of all four suites of markers illustrated that an increase in population sample size profoundly influenced accuracy of estimated stock compositions for those populations that were initially poorly estimated at smaller population sample sizes. The effect of increasing sample size was muted for those populations that were genetically distinct and relatively easy to identify at smaller population sample sizes.

The previous analysis centered on illustrating the effect of population sample size on accuracy of estimated stock compositions for five populations of varying genetic distinctiveness. Accuracy of estimated stock compositions for populations that were easily identified tended to attain asymptotic values at lower population sizes than did populations less distinct. We evaluated the relationship between an index of genetic distinctiveness and population sample size required for 95% of asymptotic values for all populations surveyed. Less genetically distinct populations, regardless of whether SNPs or microsatellites were used in estimation of stock composition, required larger population sample sizes in order for accuracy of estimated stock compositions inherent in the markers to be expressed (Figs. 5*a* and 5*b*).

Fig. 5. Mean of the five smallest pairwise F_{ST} estimates for 40 populations of sockeye salmon in British Columbia versus population sample sizes required to attain 95% of asymptotic population assignment accuracy for B23 SNPs (*a*) and B7 microsatellites (*b*).



Discussion

Comparisons within marker classes

The number of alleles observed at a microsatellite locus had a clear effect on accuracy of estimated stock compositions. The application of the T7 microsatellites with a total of 276 observed alleles produced more accurate estimates of stock composition than did application of the B7 suite of microsatellites with 142 alleles. Microsatellite loci with fewer alleles had previously been described as providing less accurate stock composition results in Pacific Rim applications for sockeye salmon (Beacham et al. 2005), Chinook salmon (Beacham et al. 2006*c*), and chum salmon (Beacham et al. 2009*b*). The results from the current study provide an additional example of microsatellites with fewer alleles providing less resolution in stock composition estimation than more polymorphic loci. Haasl and Payseur (2011) reported that highly heterozygous loci increase the ability to detect population structure, and the previous results provide empirical support for this conclusion. For SNPs, Morin et al. (2009) reported that, in an analysis of detecting population structure with simulated loci, increasing population sample size (up to 100 individuals) was beneficial, but for well differentiated populations (F_{ST} = 0.10), little increase in power was observed after 60 individuals in a population had been sampled. The T23 set of SNPs corresponded to a well defined population structure (F_{ST} = 0.15), and the increase in accuracy of estimated stock composition was limited after 60–80 fish had been sampled in a population.

Population-specific estimates of stock composition required larger baseline population sample sizes than did regional estimates, if the objective was to obtain estimates with similar levels of accuracy. This result occurred because errors in population estimation most likely occur between populations of the greatest similarity, and since there is generally a regionally based population structure in Pacific salmon, populations of the greatest similarity will occur within the same geographic region. Although stock identification allocations to specific populations may be in error, allocations to reporting regions will have a higher accuracy, negating the requirement for further reductions in sampling error for determination of population allele frequencies. Basically, the smaller the reporting unit required for stock identification applications, the lower the accuracy of the estimated stock compositions. This general result was previously outlined by Beacham et al. (2008) in an evaluation of microsatellites for stock identification applications in Yukon River Chinook salmon. If increased accuracy at the smallest reporting unit is required, then either baseline population samples size should be increased, or addition markers incorporated in the suite for stock identification applications.

Population sample size was a key factor in determining the accuracy of stock composition estimates. Kalinowski (2004) reported that little benefit was gained in increasing baseline population sample size above 100 fish, and this was true for the T23 suite of higher resolution SNPs in the current study. A population sample size of up to 160 fish generally increased accuracy for the B23 SNPs. However, for the suites of microsatellites examined, increasing sample size to at least 200 fish provided increased accuracy for both the T7 and B7 microsatellites. Winans et al. (2004) surveyed five microsatellites containing 8–21 alleles per locus in Columbia River steelhead and concluded that sampling more than 50 fish per population produced little improvement in estimated stock compositions. These results are in contrast to those of the current study. The loci surveyed by Winans et al. (2004) corresponded to many of those in the B7 suite in our study, and increased accuracy in stock composition estimates was generally observed for population sample sizes above 50 individuals. Estimates of stock composition for very distinct populations analyzed here did not benefit from increased sample sizes, but this level of distinctiveness did not appear to be prevalent in the Columbia River steelhead populations.

Comparisons between SNPs and microsatellites

High resolution of stock composition estimation may be a function of accurate estimation of allele frequencies of the genetic markers used ("sampling error"), and of the degree of genetic differentiation among populations in the suite of genetic markers applied in estimation of stock composition ("genetic error"). Both factors influence the accuracy of estimates of stock composition when applied to mixed-stock fishery samples. The number of alleles observed at a microsatellite can be an important factor in its power for stock identification. Fewer SNP alleles than microsatellite alleles were required to provide comparable levels of stock identification accuracy, in accordance with the suggestion of Smith

and Seeb (2008) that SNP alleles have a higher information content per allele than microsatellite alleles. The 14 microsatellites evaluated in the study were developed from a range of salmonid species (Chinook salmon, coho salmon, sockeye salmon, and rainbow trout) and were typically obtained from a random genomic library. They initially displayed enough polymorphism in sockeye salmon to be considered for inclusion in a suite of microsatellites, were in Hardy–Weinberg equilibrium in test populations, and currently fit on two injections for an automated DNA sequencer. The SNPs were typically derived from published expressed sequence tags libraries, and thus have greater potential to be under selection than the microsatellites, possibly accounting for the greater information content per allele compared with the microsatellites.

It is currently of interest to compare the relative power of SNPs and microsatellites for estimation of stock composition in mixed-stock salmon fisheries (PSC 2008). Comparisons between classes of markers should be centered on evaluating the genetic error included in estimated stock compositions for a particular set of markers, rather than confounding the comparison with both sampling error and genetic error. The results of our study indicate that microsatellites require larger baseline samples than SNPs to reduce sampling variation in estimation of allele frequencies and thus increase the accuracy of estimated stock compositions. In the current study, population sample size in the microsatellite baselines was required to be at least twice as large as in the SNP baselines before equivalent levels of accuracy relative to the asymptotic value were achieved. Therefore, in comparing the effectiveness of SNPs and microsatellites for stock identification estimation for Pacific salmon, larger baseline population sample sizes will be required for microsatellites than for SNPs for all species. The suites of markers used for stock identification application in the current study displayed greater genetic differentiation than is commonly observed with other Pacific salmon species (Beacham et al. 2006*b*, 2009*a*). As markers are employed in stock identification applications that display less differentiation than those in the current study, larger baseline sample sizes will likely be required than even those estimated in the current study, if similar levels of accuracy relative to the asymptotic value are to be attained.

Studies comparing stock identification power of SNPs and microsatellites that have incorporated equal population sample sizes, and with population sample sizes under the number of individuals per population required to stabilize estimates of stock composition, will have the results confounded by sampling variation. Smith and Seeb (2008), in an analysis of the power of SNPs and microsatellites for stock identification of western Alaska chum salmon (*O. keta*), surveyed 61 SNPs and 15 microsatellites, with up to 115 alleles observed at a single microsatellite. With population sample sizes of 78–96 fish, and equal numbers of individuals surveyed for both SNPs and microsatellites, relatively more sampling error will be present in estimation of microsatellite allele frequencies compared with the SNPs. With F_{ST} values of 0.006–0.047 for the microsatellites, there was limited resolution among the populations in the baseline, and it is necessary to sample considerably more than 96 fish to minimize sampling error in order that a true test of the genetic error is conducted. Narum et al. (2008), in a study of 29 populations of Chinook salmon, surveyed 96 or fewer individuals for 26 of the 29 populations included in the baseline. The experimental design again consisted of surveying equal numbers of individuals for SNPs and microsatellites, with up to 52 alleles observed at the microsatellites, and the typical two alleles at SNPs. As the results in our study indicated, determination of microsatellite allele frequencies at this level of sampling will incorporate sampling error in allele frequency estimation. This will confound the evaluation of the genetic power of the individual loci for stock identification, as we suggest that comparisons should be conducted when estimates of stock composition are relatively stable with respect to baseline population sample size. Clearly, microsatellites require more fish to be sampled in a population to obtain estimates of allele frequencies with similar accuracy and precision compared with SNPs, where only the frequencies of two alleles (one independent) are estimated. Comparison of the genetic efficacy of SNPs and microsatellites for stock identification applications requires that adequate sample sizes be available for populations included in the analyses for both classes of markers.

The current study was focused primarily on evaluating the stability of estimated stock compositions with respect to variable population size, i.e., evaluating the effect of sampling error on accuracy of estimated stock compositions for loci with varying numbers of alleles. The genetic effectiveness of the two main classes of markers investigated, SNPs and microsatellites, was not evaluated. This comparison has been conducted elsewhere for sockeye salmon in British Columbia (Beacham et al. 2010). Anderson (2010) reported that the accuracy of population assignment for a set of genetic markers can be overestimated in routine application if the suite of markers has been chosen specifically for observed allele frequency differentiation among existing population samples. Testing of accuracy would ideally occur for individuals not included as part of the baseline samples. Accuracy of estimated population-specific compositions derived from the microsatellites has been reported for a number of completely independent samples (Beacham et al. 2004, 2005), with population-specific accuracy similar to that observed in the current study. Therefore, trends in accuracy of stock composition reported in the current study were not dependent upon the specific suites of loci evaluated.

Population genetic differentiation and accuracy of estimated stock composition

The genetic distinctiveness of a particular population can influence the experimental design employed in construction of a baseline for stock identification applications. If a population is quite distinctive genetically, then greater error in estimation of allele frequencies can be tolerated for this population, and the number of fish surveyed for the genetic markers can be reduced relative to a less distinct population. The results of the current study indicated that less distinct populations required larger sample sizes to stabilize stock composition estimates in comparison with more distinct populations. Therefore, development of baselines in which a set number of fish per population is targeted, such as the 144 individuals per population as outlined by (Seeb et al.

2007), is unlikely to be the best experimental design to use if the power of the genetic markers used is to be exploited with maximum efficiency. Initial equal population sample sizes can be targeted until genetic distinctiveness of the populations in the baseline is evaluated, and then larger population sample sizes may be required for those populations and regions that are less distinct. When increased resolution of stock composition for a particular population in the baseline in mixed-stock analysis is required, two options are available: either reduce the sampling variation in estimation of allele frequencies for the particular population or reduce the error generated in applying the suite of genetic markers used in estimation of stock composition. Increasing sample size for the population is clearly the easiest route to follow, as efforts to provide greater resolution in stock composition estimates can be directed at the population in question, as well as other populations in the same reporting group. Reducing the error generated in applying a suite of genetic markers will generally require increasing the number or type of genetic markers applied, and this change must usually be instituted for all populations in the baseline.

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PERSPECTIVE / PERSPECTIVE

Genetically modified plants as fish feed ingredients

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Abstract: Genetically modified (GM) plants were first grown commercially more than 20 years ago, but their use is still controversial in some parts of the world. Many GM plant varieties are produced in large quantities globally and are approved for use in fish feeds both in Norway and the European Union. European consumers, however, are skeptical to fish produced by means of GM feed ingredients. Concerns have been raised regarding the safety of GM plants, including potential toxicity and (or) allergenicity of the novel protein, potential unintended effects, and risk of horizontal gene transfer to other species. This review will present the current state of knowledge regarding GM plants as fish feed ingredients, focusing on fish performance and health as well as the fate of the GM DNA fragments in the fish, identifying limitations of the current work and areas where further research is needed.

Résumé : Les plantes génétiquement modifiées (GM) ont commencé à être cultivées commercialement il y a plus de 20 ans, mais leur utilisation reste controversée dans certaines régions du globe. Plusieurs variétés de plantes GM sont produites en grande quantité à l'échelle mondiale et sont acceptées dans la préparation de la nourriture de poissons, tant en Norvège que dans l'Union européenne. Les consommateurs européens maintiennent cependant une certaine inquiétude concernant les poissons produits par l'usage d'ingrédients alimentaires GM. On a manifesté des préoccupations en ce qui a trait à l'innocuité des plantes GM, en particulier à la toxicité et (ou) l'allergénicité potentielles des protéines nouvelles, aux effets potentiels imprévus et au risque de transferts horizontaux des gènes aux autres espèces. Notre rétrospective résume l'état actuel des connaissances sur les plantes GM utilisées comme ingrédients dans l'alimentation des poissons, avec une emphase particulière sur la performance et la santé des poissons, ainsi que sur le sort des fragments d'ADN GM chez les poissons, tout en soulignant les limites des travaux actuels et en identifiant les domaines de recherche additionnelle nécessaire.

[Traduit par la Rédaction]

Introduction

Genetically modified (GM) plants are plants "whose genetic material is modified in a way which is not found in nature under natural conditions of crossbreed or natural recombination" (Gene Technology Act 1993). Genetic modification has been used successfully to introduce new properties in crop plants. Irrespective of the technology used, integration of the novel DNA happens through so-called illegitimate recombination (nonhomologous end-joining) rather than homologous, or site-directed, recombination (Hansen and Wright 1999; Gelvin 2003). Thus, random insertion of the novel gene might disrupt endogenous gene expression in the modified plant, which could cause unintended effects, such as changes in levels of macronutrients and (or) micronutrients, antinutritional factors, or inherent plant toxicants (Cellini et al. 2004; Somers and Makarevitch 2004). If such changes have occurred in the GM plant, they may affect the value of the plant as a feed ingredient for fish. Another concern is that the presence of the novel GM protein can affect animals consuming the plant, as exemplified by immunological reactions induced

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in mice (Prescott et al. 2005). According to Kuiper et al. (2001), a comprehensive safety assessment includes toxicity and allergenicity testing of the novel protein, molecular characterization of the insert, evaluation of unintended effects, and potential for horizontal gene transfer to other species. Safety testing of whole foods is problematic, as high doses cannot be given to experimental animals without introducing nutritional imbalances, and thus safety margins for intake are difficult to establish (Kuiper and Kleter 2003).

Since 1996, the proportion of GM crops relative to total harvest has increased rapidly. In 2008, the percentages of the global acreage of the crop plants soybean, cotton, maize, and canola planted with GM varieties were 77%, 49%, 26%, and 21%, respectively (James 2009). Consequently, it is becoming increasingly difficult for fish feed producers to obtain nonmodified varieties of certain plant products (Kaushik and Hemre 2008; Anonymous 2009).

GM plants in fish feeds

A limited number of fish feeding trials to assess GM plants as feed ingredients have been conducted (summarized in Table 1). The studies vary in their focus, as well as fish species, inclusion level and type of GM ingredients, and duration of the trials. Some studies have utilized the maternal near-isogenic line of the GM plants in their control diet, while others have used an unrelated, conventional variety. In many studies, a fishmeal reference diet has also been used to establish the normal levels of the measured parameters.

Roundup Ready (RR) soybean

Herbicide tolerance is the most common trait that GM plants have been modified for, including soybean, maize, cotton, canola, rice, sugar beet, alfalfa, wheat, cotton, and linseed (GM crop database: www.cera-gmc.org). The glyphosate-tolerant soybean variety Roundup Ready (RR) is the dominant soy variety on the market (James 2009), which makes it very relevant for inclusion in animal feeds. This soy expresses the CP4 EPSPS protein, for which no toxic effects were detected (using protein produced in an *E. coli* system) in mice fed high doses, and the protein was found to degrade rapidly in simulated gastric fluid and not be homologous to known allergens or toxins (Harrison et al. 1996). RR soy has been concluded to be compositionally equivalent to its nontransgenic parental line, irrespective of herbicide use and growing location (Padgette et al. 1996; Taylor et al. 1999; McCann et al. 2005).

In the first fish feeding trial conducted with RR soy, catfish (*Ictalurus punctatus*) fingerlings were fed a diet containing 45% GM soybean or the near-isogenic maternal line for 10 weeks (Hammond et al. 1996). Fish growth, survival, feed conversion, and fillet composition exhibited no differences between the diet groups. Similarly, no differences were observed in growth, feed performance, and whole body composition of rainbow trout (*Oncorhynchus mykiss*) fed RR soy for 3 months at 15% and 30% inclusion in the diet (Chainark et al. 2006). No further health or performance parameters were measured.

Several feeding trials with RR soy have been conducted with Atlantic salmon (*Salmo salar*). A challenge in these studies is that salmon do not tolerate high levels of most soybean products, depending on the degree of refinement. They develop an inflammatory response in the distal intestine, so-called soybean meal-induced enteritis (Van den Ingh et al. 1991; Baeverfjord and Krogdahl 1996) that can complicate evaluation of GM soybean varieties. Nonetheless, this has been done, mostly at moderate inclusion levels.

A 3-month study was conducted with Atlantic salmon fed RR soy at 17% inclusion and a diet with conventional soy and a fishmeal diet as controls (Hemre et al. 2005; Bakke-McKellep et al. 2007). The relative size of the spleen was increased in the GM-fed group compared with the non-GM-fed group, but neither were statistically different from the fishmeal control group (Hemre et al. 2005). There were no differences in growth, nutrient utilization, or in other organ indices. Haematological parameters, plasma nutrient concentrations, and leakage of organ-specific enzymes to the plasma compartment showed similar values in all dietary groups (Hemre et al. 2005). There was a tendency towards increased lysozyme activity in the head kidney of the GM-fed fish ($p = 0.06$), but no differences in soy-induced inflammations or levels of major histocompatibility complex were detected in the distal intestine of the fish fed the two soy varieties (Bakke-McKellep et al. 2007). Furthermore, there were no differences in lysozyme or immunoglobulin levels in other tissues, nor in EROD (ethoxyresorufin-*O*-deethylation) activity in liver (Bakke-McKellep et al. 2007). Samples from the distal intestine of these fish were used for construction of a suppression subtractive hybridization (SSH) cDNA library from which clones were sequenced and some followed up by qPCR to investigate differential expression between the diet groups. Only minor differences were detected (Frøystad et al. 2008). As the maternal line was not used as control, differences in the soy cultivars and growing conditions were suggested as potential confounding factors.

The spleen was also substantially larger in GM- versus non-GM-fed fish in a 28-day trial with 15% and 30% inclusion of RR soy and with the maternal, nonmodified soy-line used in the control diets (Sagstad et al. 2008). Another difference observed in this study was lower plasma triacylglycerol (TAG) levels in the GM-fed fish, which may be explained by a slight difference in saponin levels between the two soy qualities.

In a study conducted on juvenile Atlantic salmon from first feeding and with a duration of 8 months, 12.5% hybrid RR soy was added to the experimental diet, and a commercial soy diet and a fishmeal diet were used as controls (Sanden et al. 2006). Plasma TAG was found to be lower in the GM-soy-fed fish compared with those fed conventional soy. The relative masses of the intestine, spleen, liver, heart, and brain did not differ between the GM- and non-GM-soy-fed groups. Investigating the intestinal tract of these fish, Sanden et al. (2005) reported higher cell proliferation in fish fed the non-GM soy diet compared with GM soy, while both of these groups were elevated compared with the fishmeal reference diet, reflecting changes caused by the soy-induced inflammatory response. No differences were observed in lysozyme levels or immunoglobulin M in the intestinal tract. Bakke-McKellep et al. (2008) reported digestive enzyme activities, active glucose uptake, and

Table 1. Overview of fish feeding trials published in the scientific literature with genetically modified (GM) plant products.

GM plant	Fish species	GM (%)	Duration	Main effects*	Reference(s)
RRS	Catfish (*Ictalurus punctatus*)	45	10 weeks	No differences	Hammond et al. 1996
RRS	Atlantic salmon (*Salmo salar*)	17	3 months	Spleen size ↑; Lysozyme ↑	Hemre et al. 2005; Bakke-McKellep et al. 2007; Frøystad et al. 2008
RRS	Atlantic salmon	~6	8 months	Plasma TAG ↓; Cell proliferation ↓; Glucose uptake ↑	Sanden et al. 2005; Sanden et al. 2006; Bakke-McKellep et al. 2008
RRS	Rainbow trout (*Oncorhynchus mykiss*)	15, 30	3 months	No differences	Chainark et al. 2006
RRS	Atlantic salmon	15, 30	28 days	Spleen size ↑; Plasma TAG ↓	Sagstad et al. 2008
RRS	Atlantic salmon	25	7 months	Midintestine mass ↓; Plasma TAG ↑; Intestinal inflammation ↑; Liver glycogen ↓	Sissener et al. 2009*a*; Sissener et al. 2009*b*; Sissener et al. 2010*a*
RRS	Zebrafish (*Danio rerio*)	25	3 weeks	Liver RNA yield ↓	Sissener et al. 2010*b*
MON810	Atlantic salmon	~6	8 months	No differences	Sanden et al. 2005; Sanden et al. 2006; Bakke-McKellep et al. 2008
MON810	Atlantic salmon	15, 30	82 days	Feed intake ↓; Growth ↓; Liver size ↑; Distal intestine mass ↑; Glucose uptake ↑; SOD ↑; CAT ↓; Granulocytes ↑	Hemre et al. 2007; Sagstad et al. 2007; Frøystad-Saugen et al. 2009
MON810	Zebrafish	20	3 weeks	Growth ↑; SOD ↓	Sissener et al. 2010*b*
GM cotton	Catfish	20	8 weeks	Fillet protein ↓	Li et al. 2008
RR canola	Rainbow trout	5, 10, 15, 20	NA†	Protein retention ↑	Brown et al. 2003
GM lupin	Red seabream (*Pagrus auratus*)	60	40 days	Growth ↑	Glencross et al. 2003

Note: Only studies evaluating the effects of GM plants as feed ingredients are included (not studies focusing on the traceability of DNA).
RRS, Roundup Ready soy; TAG, triacylglycerol; SOD, superoxide dismutase; CAT, catalase.
*Differences between fish fed GM to fish fed non-GM plants: (↑) indicates that the parameter in question was higher in the GM-fed fish, while (↓) indicates lower values in the GM-fed group. Further details on the changes and confounding factors in the studies are discussed in the text.
†Duration of study is not clear from the paper.

SGLT1 (sodium–glucose-linked transporter) protein levels in the various intestinal regions and found the highest rate of glucose transport and SGLT1 protein levels in the pyloric caeca of fish fed GM soy, intermediate levels in non-GM soy groups, and lowest levels with the fishmeal groups. Maltase activity in the pyloric caeca was substantially lower in GM-soy-fed than non-GM-soy-fed fish.

Earlier observations of increased spleen size (Hemre et al. 2005; Sagstad et al. 2008) and lowered plasma TAG (Sanden et al. 2006; Sagstad et al. 2008) were not confirmed in a 7-month feeding trial with a relatively high inclusion level (25%) of RR soy and the near-isogenic maternal line (control), starting in the parr stage and going through the parr–smolt transformation (Sissener et al. 2009*a*). In this study, spleen mass was similar between the groups throughout the trial, and plasma TAG was found to be higher in the GM group at all samplings, although the magnitude of this difference was larger around the time of seawater transfer than later on in the trial. Furthermore, the relative mass of the midintestine was found to be lower in the GM group, something that had not been observed in the previously published trials. Other organ indices and plasma enzymes and nutrients, as well as growth, body composition, haematological values, spleen and head kidney lysozyme levels, adaptation to seawater, and stress response were not found to be different between the diet groups. Histological evaluations of internal organs revealed decreased liver glycogen deposits and indications of a more pronounced inflammation status in the distal intestine of fish fed the GM diet (Sissener et al. 2009*b*). However, intestinal inflammation was observed in both diet groups at all sampling points, as would be expected at the current inclusion level of soybean meal. Further analyses are currently being conducted to describe the differences in the degree of severity of the inflammation caused by the two soy varieties. When liver protein expression was compared between the diet groups by means of proteomics, no apparent biologically meaningful differences were detected, and the two diet groups were indistinguishable by principal component analysis (Sissener et al. 2010*a*).

A 3-week feeding trial with zebrafish (*Danio rerio*) fed

RR soy (25% of diet) and the maternal near-isogenic line has also been published (Sissener et al. 2010*b*). Liver RNA yield tended to be higher in fish fed non-GM compared with GM soy ($p = 0.06$), and there was a significant interaction effect between soy variety and the sex of the fish ($p = 0.003$). The females in the non-GM soy group seemed to have larger livers than the females in the GM soy group, while this was not the case for the males. There was also an interaction effect between soy variety and sex on liver superoxide dismutase (SOD)-1, with lowered transcription levels in females but not in males fed GM soy. These interactions indicate a difference in how the two soy varieties affect the male and female zebrafish, possibly by differentially affecting sex hormones. Soy is known to contain phytoestrogens (soy isoflavones) that can affect reproduction and vitellogenin levels in fish (Pelissero et al. 1991; Kaushik et al. 1995; Kelly and Green 2006). Unfortunately, these compounds were not measured in the soy used for this trial. There were no differences in mass, length, or condition factor, nor in the mRNA transcription of a range of other stress-related genes, such as heat shock protein 70 (*hsp70*), *hsp90*, DNA-repair protein, and glutathione peroxidase.

The lack of reproducibility or even contradictory results observed between the different fish feeding trials summarized above, even between trials using the same fish species (with salmon being the most extensively studied), suggest that these effects are not caused by the GM protein. However, they may be related to unintended effects of the genetic modification, which can result in variations in levels of antinutritional factors, antigens, metabolites, or other unidentified factors in the plants. Variations in such components also occur between batches of conventionally produced plants, as evidenced by varying levels of soybean meal-induced intestinal inflammation in salmon fed soy grown in different locations around the world (Urán et al. 2009). None of the differences observed between the diet groups have been identified as adverse, as they appear to be within the normal physiological ranges for the species, at least as far are these ranges have been identified in these fish species. A large range of health- and performance-related parameters have been investigated in fish, mainly salmon, fed RR soy, and the overall conclusion is that only minor, rather variable differences are seen, and none of the studies showed differences in growth or nutrient retention. Consequently, RR soy appears to be an equally suitable feed ingredient as conventional soy at dietary inclusion levels appropriate for the assessed fish species.

Bacillus thuringiensis (Bt)-maize

In the category of insect-resistant GM plants, plants expressing different Cry-proteins have been developed (www.cera-gmc.org). Naturally produced by the spore-forming soil bacterium *Bacillus thuringiensis*, these proteins are often referred to as Bt-proteins or Bt-toxins. The different Cry-proteins bind to specific receptors in the midintestine of their target insects, where they cause damage to the intestinal wall by forming pores and changing the permeability of epithelial cells, eventually resulting in death (Knowles 1994). Administered to mice in a dose of 4000 mg·kg^{-1} in the feed, the Cry1Ab protein caused no signs of acute toxicity (Sanders et al. 1998), but studies in mice using Cry1Ac have observed binding to mucosa, hyperpolarization of intestinal tissue, and stimulation of antibody production (Vázquez-Padrón et al. 1999 and 2000; Moreno-Fierros et al. 2000).

Regarding compositional equivalence, 10 Bt-corn hybrids were found to have higher content of lignin, a major structural component of plant cells, than their near-isogenic lines (Saxena and Stotzky 2001). Levels of mycotoxins in corn kernels may cause differences in nutritional value of Bt versus conventional maize (Munkvold et al. 1997). Despite large variations between locations and seasons, mycotoxin levels have generally been observed to be reduced in Bt-maize, as insect damage can predispose for fungal growth (e.g., Dowd 2000; Bakan et al. 2002; Papst et al. 2005). This has been used to explain higher mass gain in the GM-fed group in some studies with various production animals fed Bt-maize (reviewed by Flachowsky et al. 2005), although cause–effect relationships were not established.

Sanden et al. (2006) evaluated two different MON810 hybrids along with nonmodified controls in an 8-month feeding trial with Atlantic salmon juveniles from first feeding onwards. The inclusion level of the different maize types was 12% (GM content about 6%). Differences in response parameters in the fish were seen between the different maize types, but none appeared to be related to whether the maize was GM or not. The evaluations included assessment of growth; organ masses; plasma parameters; histological, digestive, metabolic, and immunological parameters, as well as intestinal cell proliferation (Sanden et al. 2005, 2006; Bakke-McKellep et al. 2008).

In another study, Atlantic salmon postsmolt fed GM maize (MON810) at 15% and 30% of the total diet had substantially reduced feed intake, growth rate, and final mass compared with fish fed non-GM maize (Hemre et al. 2007). Furthermore, major differences were revealed in organ indices: the relative mass of both liver and distal intestine was increased in the fish fed GM maize. Some differences were observed in head-kidney and spleen somatic indices as well, but these were not dose related and not considerably different between the GM- and non-GM-fed groups as a whole. No differences were observed during histological evaluations of the same organs. Maltase activity in the midintestinal segment of fish fed the 30% GM diet was higher than the 30% non-GM group. Uptake of glucose in pyloric caeca was also substantially higher in fish fed the GM diet, reflecting findings in salmon fed GM soy (Bakke-McKellep et al. 2008). Fish health in this trial was evaluated focusing on stress- and immune-response biomarkers (Sagstad et al. 2007). SOD had higher activity in liver and distal intestine, while catalase (CAT) showed substantially lower liver activity in fish fed GM maize. HSP70 was significantly higher in the liver of fish fed GM maize compared with the fishmeal reference diet, while the non-GM maize group exhibited intermediate levels. The differences in activity and protein levels of CAT, SOD, and HSP70 were not reflected in levels of mRNA coding for these proteins. Differential count of white blood cells revealed a considerably higher proportion of granulocytes in the blood of fish fed GM maize. The authors suggested that the GM maize MON810 caused changes in the immune response with a related mild cellular stress response. Altered liver metabolism was also indicated based

on the higher liver index and changes of CAT, HSP70, and SOD. Construction of an SSH-library from distal intestine, followed up by qPCR, revealed only minor differences between the diet groups in gene transcription (Frøystad-Saugen et al. 2009). Microarray data from liver and distal intestine of these fish are currently being evaluated.

In a 3-week zebrafish feeding trial with 20% inclusion of GM maize (MON810) and the maternal line as control, using the same batch of maize as in the salmon trial described above, better growth was observed in the GM-fed group (Sissener et al. 2010*b*). Additionally, reduced *SOD-1* mRNA levels and a tendency (nonsignificant) towards reduced *hsp70* mRNA levels were found in liver of fish fed GM compared with non-GM maize. The discrepancy of these results with those obtained in salmon (Hemre et al. 2007; Sagstad et al. 2007) is hard to explain, but could be due to differences in species, developmental stage, duration of the trials, maize inclusion levels, or feed processing.

Compared with RR soy, the data on use of Bt-maize in fish feeds are scarce, and the results in the above mentioned trials differ widely. Thus, further research is needed to conclude on whether or not Bt-maize fed to fish can have different effects on growth, stress, and immune responses compared with nonmodified maize.

GM cotton

Different varieties of GM cotton have been evaluated in diets for channel catfish (Li et al. 2008). The four GM cotton varieties evaluated were Roundup Ready Flex (expressing the CP4 ESPS protein), Bollgard × Roundup Ready (expressing both Cry1Ac and CP4 EPSPS), Bollgard II × Roundup Ready (expressing Cry1Ac, Cry2Ab2, and CP4 EPSPS), and Bollgard II × Roundup Ready Flex (expressing Cry1Ac, Cry2Ab2, and CP4 EPSPS). The three latter cotton varieties are crosses of two GM varieties, so-called stacked events combining both herbicide tolerance and insect resistance in the same plants. Nutritional evaluations of cotton seed meal (CSM) from these plants were conducted in three separate feeding experiments, all of which lasted for 8 weeks and included non-GM CSM from a genetically similar control as well as several commercial varieties as references. All diets contained 20% CSM. Chemical analyses of the various CSM varieties revealed differences in proximate composition and gossypol levels in all three trials, but these were to some extent balanced for in the feed formulation. The parameters examined were growth, survival, feed efficiency, and fillet composition. Bollgard × RR and Bollegard II × RR were both found to cause lower fish fillet protein content than the genetically similar, nonmodified CSM, while only Bollegard × RR-fed fish were substantially different from fish fed the commercial varieties as well. Despite this difference, the authors conclude that all the GM CSMs are nutritionally equivalent to nonmodified CSM (Li et al. 2008).

RR canola

Two lines of RR canola have been tested in diets for rainbow trout: modification events GT200 and GT73, both containing the gene for CP4 EPSPS and a glyphosate oxidase gene from *Ochrobactrum anthropi* that catalyses the breakdown of glyphosate. These were included in fish diets in a regression design at 5%–20% and compared with the parental line as well as a reference diet not containing canola (Brown et al. 2003). The GT200 line was equivalent to nonmodified canola as judged by fish performance, while the GT73 line resulted in increased protein retention, increased body protein and moisture, and reduced body lipid compared with the parental line. This might be due to small differences in protein content and nitrogen solubility between the canola lines, which does not seem to have been balanced for in the formulation of the diets. Specific information concerning this, as well as compositional analysis of the diets, was not supplied. The authors conclude that glyphosate-tolerant canola is equivalent to conventional canola for use in trout diets (Brown et al. 2003).

Lupin with increased methionine

The first GM plants commercialized were aimed at improving agronomical traits, such as tolerance to herbicides or resistance to insect attack. More elaborate modifications, aimed at changing the nutrient profile of the plants, are often referred to as "second generation" GM plants. The only second generation GM plant with published results in fish diets is a GM lupin variety in diets for juvenile red seabream (*Pagrus auratus*) (Glencross et al. 2003). This lupin line was modified to express a sunflower seed albumin gene leading to increased levels of methionine (Molvig et al. 1997), but has not been commercialized. Two commercial lupin varieties were used as reference, one of which was very close in proximate composition to the GM variety. A diet with this latter non-GM lupin variety fortified with crystalline methionine was also included in the experimental design. Apart from poorer growth in fish fed one of the non-GM lupin varieties, which had much lower protein content than the others, no differences were observed in an initial experiment with high protein diets and ad libitum feeding (Glencross et al. 2003). In a subsequent feeding trial with subsatietal pair-feeding and protein-restrictive diets, a beneficial effect on growth was seen with both the GM diet and the non-GM diet with added crystalline methionine when compared with the nonfortified non-GM variety.

GM plants of the future as fish feed ingredients

To our knowledge, no work has been conducted on commercialized second generation GM plants as fish feed ingredients. Attempts to tailor nutrient composition are likely to give unintended effects, as further changes are made in metabolic pathways and nutrient balance (Larkin and Harrigan 2007). This may cause altered levels of undesirable substances (e.g., anti-nutritional factors) and reduced growth in experimental animals (Böhme et al. 2005; Böhme et al. 2007). However, these GM plants do not only present challenges for the animal feed industry, but also opportunities for novel plant products better suited for specific animal species, such as fish. Few such GM plants are commercially available, but many are under development and can be expected to be introduced to the market in the coming years.

Replacement of fish oil and fishmeal by lipid and protein from vegetable sources is a necessity to make the aquaculture industry sustainable (FAO 2005). However, fish oil replacement may affect the product quality and health benefits for the consumer, as the fish fillet will contain less of the

marine long-chained polyunsaturated omega-3 fatty acids. Plants modified by introducing genes from microalgae to produce omega-3 fatty acids are under development, and commercial production is targeted to begin in 2015 (Watkins 2009). Monsanto (http://www.monsanto.com/Pages/default.aspx) has also been working on production of long-chain omega-3 fatty acids in canola (Ursin 2003).

Amino acid composition of plant proteins is another way in which plants can be modified to be more attractive as fish feed ingredients. Maize with increased level of lysine is already on the market (LY038) and has been tested with positive results in broilers (Lucas et al. 2007). Corn gluten is a promising protein source for use in fish, but low lysine level is considered a limiting factor (Aslaksen et al. 2007). Reference diets must be designed to contain lysine levels below what is required for optimal performance to avoid similar problems as experienced by Glencross et al. (2003), and an additional reference diet spiked with crystalline lysine to the same level as present in the GM plant would be a natural control. Such modifications could be very useful, as amino acids from intact protein seem to be utilized better than free amino acids in fish (Davies and Morris 1997; Sveier et al. 2001). Similarly, the usefulness of other plants proteins could be increased by genetic modification, such as increased methionine content in legumes (Müntz et al. 1998).

Antinutritional factors severely hamper performance especially in salmonid fish fed soybean meal (which is a preferred feed ingredient owing to availability and a relatively good amino acid profile considering the requirements of the fish). There are also numerous antinutrients in other plant products limiting their use in fish feeds (Francis et al. 2001). Many of these compounds have protective roles in plants; for example, for cotton, a variety without gossypol was developed through traditional breeding, but was not successful as it was highly prone to insect attack. With genetic modification, using antisense and RNAi to silence target genes in specific tissue, it was possible to eliminate gossypol production only in the seeds of cotton (Sunilkumar et al. 2006).

Uptake of transgenic DNA

One of the concerns related to the use of GM feed ingredients is the fate of the inserted DNA sequence, consisting of a transcription promoter, a coding sequence for the gene of interest, and an expression terminator. This DNA is often coupled to a marker that is used to identify successfully transformed cells, for example, antibiotic-resistant genes. There is concern related to the possible horizontal gene transfer (HGT) of intact antibiotic-resistant genes to the microflora of the intestinal tract of animals eating GM ingredients. HGT is defined as the transfer of genetic material directly to a living cell or an organism followed by its expression, a common phenomenon among prokaryotes (van den Eede et al. 2004). Most scientists conclude that these events occur at such low frequencies in nature, if at all, so that as long as one uses genes conferring resistance to antibiotics of limited clinical importance and to which resistant bacteria are already widespread both in the human gut and the environment (such as the commonly used nptII marker), there is no risk attached (Gay and Gillespie 2005; European Food Safety Authority 2009). However, there are some that disagree and criticize the sensitivity of studies conducted to detect these events. Several methods have been developed for alternative marker systems or removal of marker genes before release of GM plants (Hohn et al. 2001; Cuellar et al. 2006). Of the commercialized GM plants used in the studies described in this paper, Bollogard cotton is the only one containing an antibiotic resistance marker (nptII).

However, concern is also linked to the possibility of HGT to (eukaryotic) animals. There are numerous articles reporting on the fate of DNA from GM plants in mammals (e.g., Schubbert et al. 1998; Hohlweg and Doerfler 2001), and questions have been raised regarding the fate of GM DNA in edible products such as milk, meat, and eggs (Einspanier et al. 2001).

Modern salmonid diets produced by extrusion are subjected to mixing, shearing, and heating under high pressure. Despite this, GM DNA fragments have been detected in extruded fish diets (Sanden et al. 2004; Chainark et al. 2008). In the gastrointestinal tract (GIT) of animals, dietary DNA will be broken down to smaller monomers through the action of gastric acids and pancreatic and intestinal epithelial cell nucleases. A number of factors may influence the persistence and stability of DNA in the intestine, including the feed matrix within which the DNA is contained; for example, complex carbohydrates have been found to have a protective role (Palka-Santini et al. 2003). DNA fragments that have survived feed processing and the digestive enzymes of the GIT may potentially be absorbed into the intestinal mucosa and subsequently transported into the rest of the body. However, mechanisms of absorption are not known. Transcellular absorption of undigested macromolecules, mostly proteins, has been demonstrated in the fish intestine (Rombout et al. 1985; Buddington et al. 1997). The paracellular route involving a direct diffusion of molecules between epithelial cells could be another possible pathway (McLean and Ash 1987). The paracellular route is often associated to particular situations, such as intestinal pathologies (Sire and Vernier 1992). Additionally, the permeability of the intestine is affected by acute stress (Sundell et al. 2003), dietary lectins (Gatlin et al. 2007), saponins, and trypsin inhibitors (McLean et al. 1990). Dietary DNA might also be co-transported across intestinal cells in a complex with various feed components, as found for oligonucleotides conjugated to ligands such as cholesterol (Vlassov et al. 1994). In vitro experiments using the human intestinal cell line CaCo-2 suggests that unconjugated DNA fragments can be transported across the intestine by a transcellular route (L.E. Johannessen, K. Berdal, A. Holst-Jensen, unpublished data). Transport of DNA across CaCo-2 cells is 1000–10 000 times higher in the apical to basolateral direction than in the opposite direction, indicating active transport.

Only few studies have investigated the fate of foreign DNA ingested by fish. In Atlantic salmon force-fed high copy numbers of polymerase chain reaction (PCR)-amplified DNA fragments, foreign DNA fragments were detected in liver, kidney, and blood (Nielsen et al. 2005). Similarly, intravenously injected PCR-amplified DNA was detected in muscle, liver, kidney, and blood of salmon (Nielsen 2006). By means of in situ hybridization, dietary DNA from GM soy was identified in the epithelial cells in the salmon intes-

time, in the cells' vacuolar system, and in the lamina propria in some samples (Sanden et al. 2006). A recent study investigating the presence of the *Cauliflower mosaic virus* (CaMV) 35S promoter from GM soybeans reported DNA fragments in the leukocytes, head-kidney, and muscle of rainbow trout, but not 5 days after changing to a non-GM diet (Chainark et al. 2008). In tilapia (*Oreochromis niloticus*) fed GM soy diets, fragments of the CaMV 35S promoter were detected in a few muscle samples after continuous feeding, while none were detected 2 days after changing to a non-GM diet (Suharman et al. 2009). However, in another study with tilapia fed GM soy, GM DNA was still detected in all organs investigated after 2 weeks of fasting (Ran et al. 2009).

In a zebrafish study, dietary DNA fragments from *rubisco* (a multicopy plant gene) and from MON810 were detected in several organs, while RR soy DNA fragments were not detected (Sissener et al. 2010*b*). This is in agreement with studies in other species, supporting the observation that dietary DNA uptake is not a specific property of GM DNA sequences, but occurs also with DNA fragments from conventional feed ingredients (Hohlweg and Doerfler 2001; Phipps et al. 2003; Reuter and Aulrich 2003). Furthermore, the GM insert does not modify the uptake of other dietary DNA fragments (Reuter and Aulrich 2003; Mazza et al. 2005). However, there seems to be differences in the degradation or uptake of different DNA fragments, possibly depending on nucleotide sequence, methylation patterns, or simply the feed matrix (Sissener et al. 2010*b*).

Common for all these studies is that some dietary DNA seems to survive the harsh conditions of feed preparation and also that dietary DNA fragments can be taken up in the intestine and be detected in internal organs of the fish. The fragments detected have generally been below a size likely to code for functional proteins (Jonas et al. 2001), but longer fragments were not searched for. The data currently available do not assess the potential for horizontal gene transfer, either to the fish itself or to microflora in the intestine. Additionally, the mechanisms and the possible function (positive or negative) of such uptake in fish or other animal species are not known. Further research on specific mechanisms of dietary DNA uptake specifically aiming to recognize what intestinal cell types are involved is needed.

Feeding trials with fish: limitations and challenges

The feeding trials discussed in this paper vary widely in their focus, inclusion of GM ingredients, duration of trials, choice of reference diets, and what response parameters are measured in the fish. There is no general consensus regarding these issues, nor on whether feeding trials are indeed necessary (Knudsen and Poulsen 2007; European Food Safety Authority 2008). The fact that some fish species, especially carnivorous fish such as salmon, are very sensitive to certain plant components compared with terrestrial production animals can certainly be used as an argument in favour of evaluating GM feed ingredients in fish. However, the general lack of information regarding which plant antinutrients or other plant components (regardless of whether the plant is GM or not), and at what level, will cause problems in fish is still a drawback. That some antinutrients interact with each other, affecting tolerance levels and what detrimental effects may occur, makes it even more difficult to predict effects in fish (Francis et al. 2001). Thus, it would be difficult to predict effects solely based on chemical analysis of the GM plant. Since unintended effects with subsequent differences in endogenous components in GM compared with non-GM plants may account for differences in responses observed in fish feeding trials, more research is needed to identify such components and their effects in fish.

Regarding what endpoints to assess in the fish, in a time with increasing focus on fish welfare, focusing solely on production parameters such as survival, growth, and fillet composition might not be enough for sceptical consumers. More sensitive parameters than growth and survival need to be included in the evaluation to be able to assess health status and detect early stage differences that might become adverse using suboptimal diets for prolonged periods of time (e.g., throughout the life cycle of the fish in an aquaculture setting). Untargeted screening techniques such as microarray and proteomics could be useful approaches both as tools to screen for unintended effects in the GM plant – GM feed and in fish target organs.

Another problem is how and what to use as a control in the trial. The near-isogenic maternal line grown under similar conditions as the GM crop is recognized as the recommended control (European Food Safety Authority 2006). Despite this, differences in the proximate composition between GM and maternal non-GM lines of CSM, canola, and soy used in fish trials described in this paper were identified (Brown et al. 2003; Li et al. 2008; Sagstad et al. 2008). This shows that even such closely related and produced crops are not identical in composition. The question then arises on how to interpret minor differences found in measured parameters in the experimental animals. How can one distinguish whether these are due to the GM protein, unintended effects of the genetic modification, or unrelated random differences in plant cultivars that might vary from one growing season or location to the next? Faced with this dilemma, it might be preferable to use several commercial non-GM cultivars as controls in the safety assessments of GM ingredients. Thus, one could establish if the parameters measured in animals fed GM plants are within the normal range of animals fed unmodified crops (European Food Safety Authority 2008). The disadvantage is that this would greatly increase the cost of trials, as well as the number of experimental animals needed. In addition to establishing whether a response is within the normal range, there is the issue of false discoveries. When many different parameters are tested, there is a greater risk that significant changes are detected because of chance alone. (On the other hand, real effects might not be detected because of insufficient power of the experiment.) Wilson et al. (2001) provide a list of questions for assessing the biological relevance of differences detected in toxicological studies, which could also be useful for GM safety assessment: (*i*) whether the trends are dose-related, (*ii*) whether they are reproducible, (*iii*) whether there is a relationship to other findings, and (*iv*) whether the magnitude of the differences suggest that they are biologically important.

Regarding diet formulation, it is crucial to ensure that the

diets are equivalent both in proximate composition and in other compounds that are relevant to the growth and health of the experimental animals. However, there will always be compounds in the feed that are not analysed, and there will be differences in the dietary ingredients that are not possible to balance in the feed formulation. Examples include antinutrients such as phytoestrogens or saponins, variable levels of naturally occurring compounds such as mycotoxins, or herbicide and pesticide residues. Residues of these compounds might explain some of the differences observed between feeding trials, or at least knowing whether or not there are such differences would better enable us to separate "GM effects" from effects caused by confounding factors. Furthermore, the levels of GM protein expression in the plant ingredients are rarely quantified, and differences between different batches of GM plants in this respect might also explain some of the discrepancies observed between feeding trials. Quantifying the transgenic protein and using an additional control diet spiked with the transgenic protein would be necessary to be able to distinguish between unintended and intended effects of the genetic modification (European Food Safety Authority 2008).

Adequate control diets already present a challenge in GM safety assessments, but this problem will most likely increase in the future, with stacked event GM plants (crosses of two or several modification events) and second generation GM plants with intended changes in nutrient composition.

Conclusions

Among the herbicide-tolerant GM plants, only RR plants have been evaluated for use in fish feeds, most extensively in salmon, but some data also exist from channel catfish, rainbow trout, and zebrafish. RR soy is the most extensively evaluated and appears to possess similar qualities as nonmodified, conventional soy products as a feed ingredient for fish. Minor or no differences were observed in the different trials, and these were not consistent from one trial to the next. Results from RR canola and cotton also show no or minor differences between diet groups.

Among the insect-resistant (Bt) plants, data are more scant and inconclusive, both as less research has been carried out and more pronounced differences have been observed between fish fed Bt-maize and conventional maize. The cause of these differences is not clear and should be followed up, including a thorough evaluation of possible effects of the Bt-protein on the fish intestine and on growth, cellular stress, and immune responses. Bt-CSM showed minimal differences from conventional CSM on growth, survival, feed efficiency, and fillet composition in channel catfish, but more specific health parameters were not evaluated.

The difference in results from the feeding trials conducted with RR soy and Bt-maize clearly shows that evaluation of one GM variety cannot automatically be extrapolated to make conclusions on the safety of other GM plants. Thus, each modification event should be considered unique, with the insertion of target genes coding for proteins that have different characteristics and with the potential occurrence of different unintended changes in nutrient or antinutrient composition. Case-by-case assessment has been advocated by others (Kuiper et al. 2001; Larkin and Harrigan 2007) and is the norm both in Norway (Norwegian Food Safety Authority) and the European Union (European Food Safety Authority).

Second generation GM plants have potential, since plant products with a nutritional profile more tailored to the specific needs of the fish can be developed, but they will also present additional challenges regarding safety assessment.

Dietary DNA fragments, including transgenic ones, withstand fish feed processing and intestinal digestion and can be absorbed by the intestine and further distributed to various tissues in the fish. The present results give no reason to suspect that transgenic sequences are taken up more frequently than regular plant DNA, or that this uptake causes any negative effects for the fish. However, the mechanisms and possible function of dietary DNA uptake in the intestine are unknown, as are types of cells involved and potential consequences of this uptake. The possibility for horizontal or vertical gene transfer has not been evaluated in fish.

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